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UNIVERSITY OF ALBERTA

Spawning and overwintering movements and habitat use by cutthroat trout (*Oncorhynchus clarki*) in the Ram River, Alberta

BY ©

Richard S. Brown

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

Department of Zoology

Edmonton, Alberta

Fall 1994

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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Spawning and overwintering movements and habitat use by cutthroat trout (*Oncorhynchus clarki*) in the Ram River, Alberta** submitted by **Richard S. Brown** in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE.**

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Abstract

Spawning movements of cutthroat trout were evaluated using radiotelemetry in a montane river and a headwater tributary. The movements of 23 fish were monitored in spring 1991 and 1992. Fish moved upstream and downstream to spawning areas. The pre- and post-spawning movements made by fish that spawned in tributaries were longer than those of fish that spawned in the mainstem or sidechannels of the main river or headwater stream. Fish moved frequently during spawning, but stayed within a small area that included several spawning sites. Trout also moved both up and downstream after spawning. In both drainages, after fish finished their post-spawning movements, they stayed within a 400 m area until observations were ended. In both pre- and post-spawning movements I found two patterns, one of fish migrating to spawning locations in tributaries (migratory), and one of fish spawning in the river or stream where they reside all year (resident).

Fall and winter movement and habitat use by trout were evaluated using radiotelemetry in low, mid, and high altitudes of a river system to evaluate what habitat shifts occurred when fish moved from summer feeding areas to overwintering areas. The movements of 45 fish were monitored throughout the fall and winter of 1991 and 1992. Cutthroat trout exhibited a two-stage shift in habitat use from summer to winter. In August and early September, trout used a wide range of habitats including pools, riffles, and runs, but in the last half of September, trout left shallower habitats and aggregated in large pools which had abundant cover. When anchor ice excluded fish from these pools in mid-November, trout moved to overwintering areas less likely to be influenced by frazil and anchor ice. These overwintering areas included deep pools, with ice cover, or areas where water temperatures were higher than the rest of the stream due to springs or upwelling warm water. Use and preference of

macrohabitat, water depth, cover, and substrate changed seasonally. Due to decreases in water discharge and exclusion of habitat by anchor ice, trout were forced into small amounts of suitable habitat leading to large aggregations.

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Chapter One

General Introduction

General Introduction

Two of the major factors limiting growth and maintenance of trout populations are reproductive and overwintering success. Reproductive success is necessary for trout to replace themselves and to increase in numbers. Routes to spawning areas must not be blocked, and adequate spawning habitat must be available. However, for populations to sustain themselves and grow, it is not enough to just have successful reproduction. It is also necessary for trout to survive the winter, the season which appears to cause severe limitations to the size of trout populations. This is because availability of suitable overwintering habitat may be limiting, however, the knowledge of trout overwintering habitat is poor.

The extent of movement that cutthroat trout (*Oncorhynchus clarki* (Richardson 1836)) make associated with spawning and overwintering is variable. Migrations are common in the spring, to spawning areas, and in the fall, to overwintering areas. River and lake resident cutthroat trout make the longest spawning migrations, over 200 km (Shepard *et al.* 1984), while stream resident trout move small distances to spawn in areas within their home stream (Varley and Gresswell 1988). Movements of cutthroat trout to overwintering areas have only been studied intensively by Heggenes *et al.* (1991b). Heggenes' (1991a) research was done in a small coastal British Columbia stream. Since air temperatures only occasionally fell below 1°C in their study area, it is likely that the movements seen there may be different from cutthroat trout in interior areas, often found in high altitude, high gradient rivers and streams subject to extremely low winter temperatures. Fish in interior areas may have to migrate more than coastal populations to avoid winter ice conditions.

Habitat use by cutthroat trout is highly variable over the course of a year. In the spring, cutthroat trout leave overwintering habitat to spawn in areas where mean substrate sizes range from 2 to 76 mm diameter, mean depths range from 17 to 22 cm, and water velocities range from 30 to 52.5 cm/sec (Cope 1957; Hooper 1973; Allan 1978; Shepard *et al.* 1984; Varley and Gresswell 1988). In the summer, cutthroat trout are primarily pool dwellers (Shepard 1983). In the fall, as temperatures cool, feeding decreases, and trout may move to areas that differ from their summer habitat. In some areas (coastal British Columbia), cutthroat trout use less cover during the winter and move out of the larger pools they use during the summer to overwinter in more shallow stream areas (Heggenes 1991a). In contrast, in streams and rivers of the Rocky Mountains of Alberta, cutthroat trout of all age classes were found aggregating in long, deep pools in the winter (Allan 1978). Other than the work of Heggenes *et al.* (1991a) and a few observations by Allan (1978) there is no information on habitat use by cutthroat trout in the winter.

Our primary objective was to evaluate the spawning and overwintering movements and habitat use by cutthroat trout in a high elevation river system exposed to large annual fluctuations in water discharge. I designed a study to investigate habitat use of individual fish as they moved from one habitat to another. Movements are often made to fulfill habitat needs, whether it be for spawning, feeding, or shelter in winter. I also chose a method (radiotelemetry) which would allow us to gather temporal data on movements and associated habitat use by individual fish. Past movement studies involved marking and recapturing cutthroat trout. While these studies reveal valuable information about movements, they rarely consider the day to day movements and behaviour during migrations.

Radiotelemetry and ultrasonic transmitters have previously been used to obtain information on spawning movements of salmonids (Bagliniere *et al.* 1990; Gray and Haynes 1979) including cutthroat trout (McCleave and Horrall 1970). There is only one study, however, which examined cutthroat trout spawning movements in rivers (Green *et al.* 1983). This research focused on how diversion dams impeded the spawning migrations of stocked cutthroat trout in a Nevada river.

It is the goal of Chapter 2 of this thesis to examine the movements to and from spawning areas, and to examine their timing. It is the goal of Chapter 3 to examine movements from summer habitat to overwintering areas, and to examine the type of habitat that trout use and prefer during fall and winter.

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Chapter Two

Spawning ecology of cutthroat trout in the Ram River, Alberta

Introduction

Little quantitative information is available on the extent and patterns of spawning related movements of trout. Radiotelemetry provides a powerful technique for quantitative evaluation of spawning related movements, but until now its potential has not been exploited for this purpose. Spawning movements of cutthroat trout have been studied by tagging and recapturing fish (Johnson 1963; Bjornn and Mallet 1964), and by trapping fish during spawning migrations (Cope 1956; Platts 1959; Johnson 1963; Huston 1973; Allan 1978). Despite these studies, there are still several important aspects of spawning biology to be explored. Among these aspects are the timing, distances, and patterns of spawning movements made by cutthroat trout.

Cutthroat trout spawn from May through July (Cope 1956; Platts 1959; Johnson 1963; Bjornn and Mallet 1964; Huston 1973; Allan 1978). They have been found moving upstream to spawning areas (up to 212 km, Shepard *et al.* 1984) triggered by increasing water discharge and temperatures and showing a strong homing instinct. Although the information obtained by trapping and tag-recapture studies is helpful, it does not give a quantitative description of movements, and only provides data at a small number of sites. A more complete picture of movements associated with spawning is possible using radiotelemetry, allowing managers to find direction, distance, and speed of individual spawning movements and to determine what factors stimulate or suppress these movements.

While radiotelemetry is a powerful tool for evaluating spawning related movements of salmonids and could be used to fill many information gaps concerning spawning biology, it has not been widely used for such studies. Radiotelemetry has been used to obtain information on spawning movements of salmonids such as Atlantic salmon (*Salmo salar* (Linnaeus, 1758)) (Bagliniere *et al.* 1990) and chinook salmon (*Oncorhynchus tshawytscha* (Walbaum, 1792)) (Gray and Haynes 1979). Ultrasonic transmitters have been used to study orientation of cutthroat trout in lakes (McCleave and Horrall 1970), but there has only been one study using radiotelemetry to study spawning movements of cutthroat trout in rivers and streams (Green *et al.* 1983). This study was done on stocked fish in a Nevada river. This research focused on how diversion dams impeded the spawning migrations of cutthroat trout. They found that most radiotagged cutthroat moved upstream to spawning areas. This study reported a high rate of mortality from transmitter implantation which hampered the effectiveness of the project.

The patterns of movements to spawning areas seen in cutthroat trout appear to be related to its place of residence or life history type. Fluvial or resident fish, which live in the headwaters of river systems, usually move little to spawning areas (Liknes and Graham 1988; Varley and Gresswell 1988). There are two migratory life history types. Fluvial-adfluvial fish live in rivers and migrate to tributary streams to spawn (Liknes and Graham 1988; Varley and Gresswell 1988). Adfluvial fish live in lakes and migrate up or downstream into rivers or streams to spawn (Liknes and Graham 1988; Varley and Gresswell 1988).

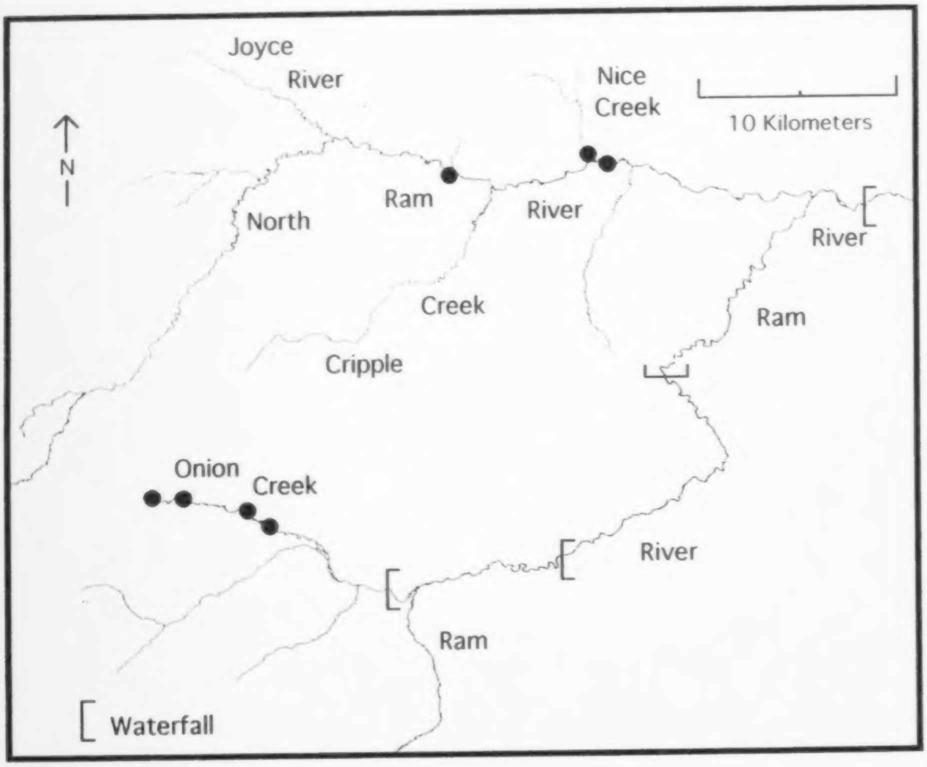
The type of life history pattern that a trout population exhibits will determine the distances they move to spawning areas. The purpose of this study was to quantify spawning movements and to gain a better understanding of spawning patterns by comparing trout populations which reside in two types of habitat; a montane river and a headwater tributary. I hypothesized that trout in the headwater tributary would exhibit a resident pattern and all would spawn within the stream, while trout in the river would exhibit a migratory behaviour and move upstream into tributaries to spawn. To achieve an accurate account of movements I used radiotelemetry.

Study Area

Within the Ram River drainage (Figure 2-1), spawning movements of cutthroat trout were compared in two different settings, a low gradient, high elevation stream, Onion Creek (tributary of the Ram River, elevation 1700-2100 m; latitude 52° 05' - 52° 8' N, longitude 116° 01' - 116° 10' W), and a higher gradient, lower elevation river system, the North Ram drainage (elevation 1250-1600 m; latitude 52° 08' - 52° 20' N, longitude 115° 40' - 116° 05' W). Onion Creek is a second order tributary (as indicated by 1:50,000 National Topography Survey Maps) and ranges in width from 0.5 m at its upstream end to 10 m near its mouth. The substrate in Onion Creek is primarily gravel and cobble. The North Ram River is fourth order from its confluence with Cripple Creek to the upper limit of the study area (the confluence of Kiska Creek), and is a fifth order stream downstream from the confluence with Cripple Creek (as shown on 1:50,000 National Topography Survey Maps). It varies in width from approximately 10 to 30 m, with substrate primarily made up of gravel, cobble, and rubble. Several of the pools in the North Ram River, however, are influenced by bedrock where the river runs along the edge of the valley. The average gradient of the North Ram River is 10.9 meters per kilometer, and the average gradient of Onion Creek is 8.1 meters per kilometer.

The flow regimes differ between Onion Creek and the North Ram River drainage. The North Ram River is a high gradient river primarily fed by runoff with highly fluctuating water discharge during the spawning period (Figure 2-2). Onion Creek is a lower gradient system surrounded by fen and it is largely fed by springs. During the spawning period it has a much more stable flow regime than the North Ram drainage (Figure 2-2).

Onion Creek is also more meandering than the North Ram River, having a sinuosity index of 1.6 while the North Ram River has a sinuosity index of 1.3.


Joyce
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10 Kilometers
N
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River
North
River
Creek
Ram
Cripple
Onion
Creek
River
Ram
Waterfall

Figure 2-1. Map of the Ram River drainage (latitude, 52° 07' N - 52° 15' N; longitude, 116° 14' W - 115° 37' W; elevation 2100 m - 1250 m). Release points of 23 radio-tagged cutthroat trout are shown as solid circles in Onion Creek and the North Ram drainage, Alberta. Fish were tracked during May and June of 1991 and 1992.

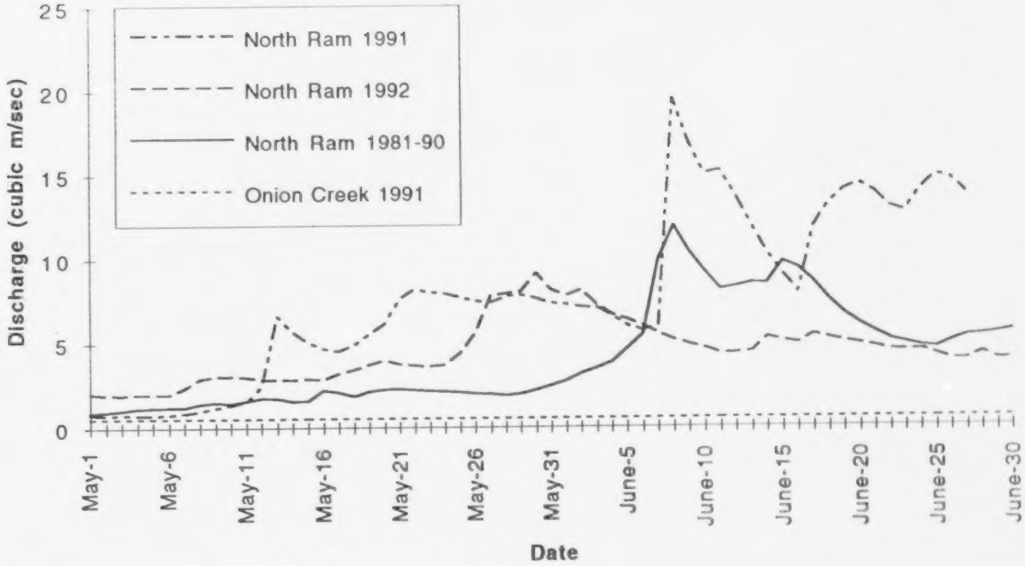

Figure 2-2. Spring water discharge (m^3/s) in the North Ram River and Onion Creek, Alberta. The water discharge in the North Ram River as measured by the Environment Canada water gauging station No. 05DC011 located in the study section. The historical mean annual runoff event was graphed (from 1981-1990 data from the gauging station) by aligning the peak flow on the mean date of peak flow. The daily mean discharges were then calculated across the 10 year period. The discharge levels for Onion Creek were calculated using staff gauge measurements.

Within the study area, the degree of sinuosity decreases in both drainages as the stream or river approaches its mouth.

Access by fish to both the Onion Creek and the North Ram system is limited by waterfalls (Figure 2-1). These waterfalls restrict fish from making long migrations downstream, isolate the two systems from each other, and determine the composition of fish species upstream of the waterfalls. Before stocking with cutthroat trout (*Oncorhynchus clarki lewisi*), their is no reported occurance of fish in the North Ram River and Onion Creek drainages because waterfalls downstream blocked immigration. The North Ram River and Onion Creek drainages were originally stocked with cutthroat trout in 1955 and restocked in 1961 and 1970 (Allan 1978). Stocked fish originated from southeastern British Columbia (Dolsen and Butler 1986).

Other than the stocked cutthroat trout, there are only two species of fish present in these waters; longnose dace (*Rhinichthys cataractae* (Valenciennes, 1842)) and longnose suckers (*Catostomus catostomus* (Forster, 1773)) (Rhude 1988). The dace and suckers were probably introduced while being used for bait. Very few dace or suckers are present in the drainage.

Methods

Twenty-three cutthroat trout were captured and implanted with radiotransmitters in four areas of Onion Creek and in three areas of the North Ram system (Figure 2-1). I hypothesized that implanted trout would move upstream to spawning areas. To test this hypothesis, in the North Ram River I captured fish from both above, below, and between tributary streams. In Onion Creek, fish were implanted in the upper, middle, and lower reaches to test our hypothesis. Thus, in both drainages, trout could move either upstream or downstream to spawning areas or spawn in areas where they were captured and likely overwintered. While trying to satisfy these general guidelines, fish were caught in the areas where they were available.

The spawning movements of 23 sexually mature cutthroat trout were monitored. Data were obtained from 22 fish in 1992, and from one fish in 1991. Twelve cutthroat trout from the North Ram River were implanted with transmitters on April 28 and 29, 1992. These trout were captured by boat electrofishing. Ten cutthroat trout from Onion Creek were implanted with transmitters between April 30 and May 5, 1992. These trout were captured by backpack electrofishing and angling. The one cutthroat trout tracked in 1991 was captured May 28 in an upstream trap located in Nice Creek near its mouth (Figure 2-1). Length, weight, sex, location of capture, and release date of implanted fish are shown in Table 2-1.

After their capture, fish were anaesthetized with a 200 mg/liter solution of tricaine methane sulfonate (MS-222) (Bidgood 1980) until the fish made no movement when the caudal peduncle was firmly squeezed (approximately 3 minutes). The fish was then laid ventral side up in a groove which was cut in a piece of soft wet foam rubber, or it was laid on a wet towel, which had the ends rolled up to form a groove (Hop *et al.* 1986). A 1-2 cm incision was made on the ventral side of the fish, anterior and slightly ventral to either of the pelvic fins. The incision was only made large enough for the transmitter to fit through, approximately 1.5-2.0 cm long. The sex of the fish was determined by observing the ripening gonads through the incision. Transmitters were coated with beeswax (Helm and Tyus 1992) before insertion into the body cavity.

The transmitters used had an external antenna (24 cm long and Teflon coated) which trailed in the water, leaving the body cavity just posterior to the pelvic fins. The antenna was threaded through the body wall using a special device; a 20 cm long, 2 mm diameter, metal rod was used to puncture the body

Table 2-1. Length, weight, sex, date of implantation, and location of release sites of 23 radiotagged cutthroat trout from the North Ram River and Onion Creek, spring 1991 and 1992. The site column indicates the location of tagging by the kilometer above the confluence with the South Ram River for fish in the North Ram River, and kilometer above the confluence with Hummingbird Creek for fish in Onion Creek.

Fish #	Site	Date Implanted	Length FL (mm)	Weight (gm)	Sex
1	NR (Nice Cr.)	May 28, 91	347	464	Male
2	NR 12	April 28	346	600	Female
3	NR 12	April 28	410	938	Female
4	NR 12	April 28	352	526	Male
5	NR 12	April 28	440	1100	Male
6	NR 12	April 28	359	692	Female
7	NR 13	April 28	401	772	Male
8	NR 13	April 28	327	460	Female
9	NR 13	April 28	343	432	Female
10	NR 22	April 28	380	640	Female
11	NR 24	April 27	314	340	Male
12	NR 24	April 27	292	264	Male
13	NR 24	April 27	268	202	Male
14	ON 5	May 5	254	178	Male
15	ON 5	May 5	250	186	Male
16	ON 7	April 30	238	150	Male
17	ON 7	May 5	273	208	Male
18	ON 7	April 30	232	164	Female
19	ON 13	April 30	294	280	Female
20	ON 13	April 30	279	292	Male
21	ON 15	April 30	287	290	Female
22	ON 15	April 30	330	410	Male
23	ON 15	April 30	301	280	Female

wall. The rod was bent at a 30° angle 5 cm from the sharp-pointed end. A 20 cm piece of polyethylene tubing (2.08 mm diameter) was attached to the long blunt end of the rod. The sharpened end of the rod was passed through the incision, and guided back through the peritoneal cavity. The rod was pushed through the body wall posterior to the pelvic fins of the fish. The rod was then pulled through the body wall. The antennae of the transmitter was guided into the tubing and as the rod and the tubing were pulled through the body wall, the antenna was guided through as well. The transmitter was then gently pushed through the incision and into the peritoneal cavity. Terramycin powder was then sprinkled into the incision.

The incision was closed using three individual sutures. Ethicon #678 sutures were used. The sutures were composed of a reverse cutting needle (3/6" circle curvature) with 18 inches of 0 silk attached. A double surgical knot was made, followed by a single and then another double surgical knot.

The entire operation (including anesthesia) took 10-15 minutes. During the operation, the fish was sprayed with water from the stream and anesthetic from spray bottles to keep the body surface moist and maintain anesthesia (Hop *et al.* 1986). If the fish's opercule stopped pulsating, the gills were sprayed with water from the stream (Hop *et al.* 1986). After the operation, the fish was allowed to recover in a bucket containing stream water or placed in calm water along the margin of the stream, until it recovered and swam away (5-10 minutes). The anesthesia and surgery did not have any obvious negative effects on the fish.

During the spring of 1992, the trout were located every second day from the time of release (April 28-May 5) until June 28. During spring 1991, one fish was located at least once a day while in the tributary stream, and then every 1-3 days after it moved downstream into the North Ram River.

Two types of transmitters were used to monitor fish movements. The first type weighed 3.0 grams in air (1.8 g in water) and had a predicted life of 50 days (Model 393 transmitters; Advanced Telemetry Systems Inc., Isante, Minnesota). The second type weighed 3.5 grams in air (2.1 g in water) and had a predicted life of 110 days (Model 357 transmitters; Advanced Telemetry Systems Inc.). The smaller transmitters were used in smaller fish to minimize the transmitter weight (in water) to body weight ratio in smaller fish. A common unpublished guideline suggests that the transmitter weight in water make up no more than 2 % of the fish's body weight. This is because the increased weight added to the fish's body by the addition of the transmitter must be made up for by the fish's increasing the size of its air bladder. Each of the transmitters emitted 54-63 pulses per minute at a different frequency between 150.000 and 150.160 MHz. A Fieldmaster radio receiver (Advance Telemetry Systems Inc.) was used to locate fish.

Fish locations were fixed with a three element YAGI antenna and recorded on aerial photographs (scale 1:5000 or 1:3750). The accuracy of the locating method was frequently checked by visually finding the fish, and was estimated to be within 0.5 m. When the locations of the implanted fish were recorded on the aerial photographs, however, the accuracy decreased from 0.5 m to approximately 5 m. Because of this, if the fish moved more than five meters between locations, it was recorded as a movement.

In 1992, water temperatures were recorded with a Ryan recording thermograph.

Data for distances moved by fish, and length and weight of fish were tested for normality using a Lilliefors test (SYSTAT 1992) and were tested to see if variance differed significantly ($P<0.05$) using an F-test. If data were normal and variances did not differ significantly ($P<0.05$) then data were analyzed using a t-test, otherwise data were analyzed using a Mann-Whitney U-Test (SYSTAT 1992). A chi-squared test (Statview 1986) was used to determine when significant differences existed in the number of moves made when water temperature or water discharge were above or below mean values. Distributions of dates when fish were first observed spawning and altitudes of fish when first spawning occurred were analyzed for normality and differences in variances as mentioned above. Correlations between altitude and date of first spawning and weight of fish were made using a Spearman's Rank Correlation (Statview 1986).

Results

Pre-spawn Movements

North Ram River

Fish moved both upstream and downstream to spawning areas. Two trout which were tagged upstream of Cripple Creek moved downstream to spawn in Nice or Cripple Creek. Most (6 of 9) fish, however, moved upstream to spawning areas. Two of these fish moved upstream to spawn in either Nice or Cripple Creeks, making a total of 4 of 9 fish that moved into tributary streams to spawn. The rest of the fish were observed (4 fish) or suspected (1 fish) to have spawned in the North Ram River or its side channels.

Five of nine radiotagged trout moved less than 1.0 km from their site of capture to spawning areas. These were all fish that spawned in the mainstem or sidechannels of the North Ram River. The mean of the distances that fish moved from capture sites to spawning areas was 3.0 km, the median distance was 0.9 km, and the maximum distance was 8.4 km (Table 2-2).

The pre-spawning movements made by fish that spawned in tributaries were significantly ($P<0.05$) longer than those of fish that spawned in the mainstem or sidechannels of the North Ram River. Trout that spawned in the mainstem or

Table 2-2. Direction and distances moved during pre- and post-spawning movements by radiotagged cutthroat trout in the North Ram River and Onion Creek, April - June, 1991 and 1992. The fish number corresponds to Table 2-1.

Fish	Site	Date	Pre-spawning		Date First	Post-spawning		Date Last
NO.		Implanted	Direction	Distance (km)	Spawning	Direction	Distance (km)	located
1	NR	May 28, 1991			June 2	Down	2.5[†]	June 27
2	NR 12	Apr. 28	Up	3.5[†]	May 19	Down	10.0[†]	June 28
3	NR 12	Apr. 28	Up	0.4	May 11	Up	0.6	June 28
4	NR 12	Apr. 28	Up	7.2[†]	May 14	Down	10.9[†]	May 31[*]
5	NR 12	Apr. 28	Up	0.1	May 17	Down	0.2	June 28
6	NR 12	Apr. 28	Up	0.3	May 4	Up	2.0	June 28
7	NR 13	Apr. 27	Down	0.9	June 9	Down	6.4	June 28
8	NR 13	Apr. 28	Up	0.6	May 17	Down	4.1	June 7[*]
9	NR 13	Apr. 28						May 29[+]
10	NR 22	Apr. 28	Down	5.3[†]	May 8	Down	10.0[†]	June 28
11	NR 24	Apr. 27	Down	8.4[†]				May 23[+]
12	NR 24	Apr. 27						May 2[+]
13	NR 24	Apr. 27						May 6[#]
14	ON 5	May 5	Up	1.2	May 18	Up	0.1	June 28
15	ON 5	May 5	Up	0.8	May 18	Up	2.5	June 28
16	ON 7	Apr. 30	Down	3.1	May 24	None	0.0	June 28
17	ON 7	May 5	Down	0.3	May 12	Up	0.03	June 28
18	ON 7	April 30						May 18[*]
19	ON 13	Apr. 30	Down	6.6	May 24	Down	2.1	June 26[*]
20	ON 13	Apr. 30	Down	0.3	June 1	Up	2.4	June 28
21	ON 15	Apr. 30						June 15[*]
22	ON 15	Apr. 30	Down	4.4	May 24	Up	2.5	June 28
23	ON 15	Apr. 30	Down	5.7	May 18	Up	0.03	June 28

[†] The fish spawned in a tributary of the North Ram River.
[*] The fish was found dead at time of last location.
[+] The fish was lost after time of last location.
[#] The fish was lost to predation.

sidechannels (N=5) made mean pre-spawning movements of 0.46 km (median 0.4 km; maximum 0.9 km) while trout that spawned in tributaries (N=4) made mean pre-spawning movements of 6.1 km (median 6.3 km; maximum 8.4 km; Table 2-2). Although tributary spawners made longer movements than mainstem and sidechannel spawners, the fish were not significantly different in length (N=9; $P>0.05$) or weight (N=9; $P>0.05$).

The timing of pre-spawning movement was related to water temperature (Figure 2-3). Pre-spawning movements were significantly longer (N=186; $P<0.05$; mean distance moved 0.55 km, median 0.18 km) when water temperatures were above the mean (8.7°C; mean maximum daily water temperature for May 1-June 9, period when all pre-spawning movements occurred) than when water temperatures were below the mean (mean distance moved 0.25 km, median 0.04 km). The number of movements that occurred when water temperatures were above the mean, however, were not significantly different (N=186; $P>0.05$) from the number of movements made when water temperatures were below the mean.

There was also a relationship between pre-spawning movements and changes in stream discharge. Significantly fewer (N=186; $P<0.05$) pre-spawning movements were made when water discharge was above the mean (mean fluctuation in water discharge between consecutive days was 0.35 m^3/s for the pre-spawning period, May 1-June 9), than during periods of stable flow. The distance of pre-spawning movements when discharge fluctuations were above the mean (>0.35 m^3/s), however, were not significantly different (N=186; $P>0.05$) from the distance moved during periods of stable flow.

Onion Creek

The cutthroat trout in Onion Creek also did not display a uniform pattern of movement to spawning areas. Fish moved both upstream (2 of 8) and downstream (6 of 8) to spawning areas. Unlike fish in the North Ram River,

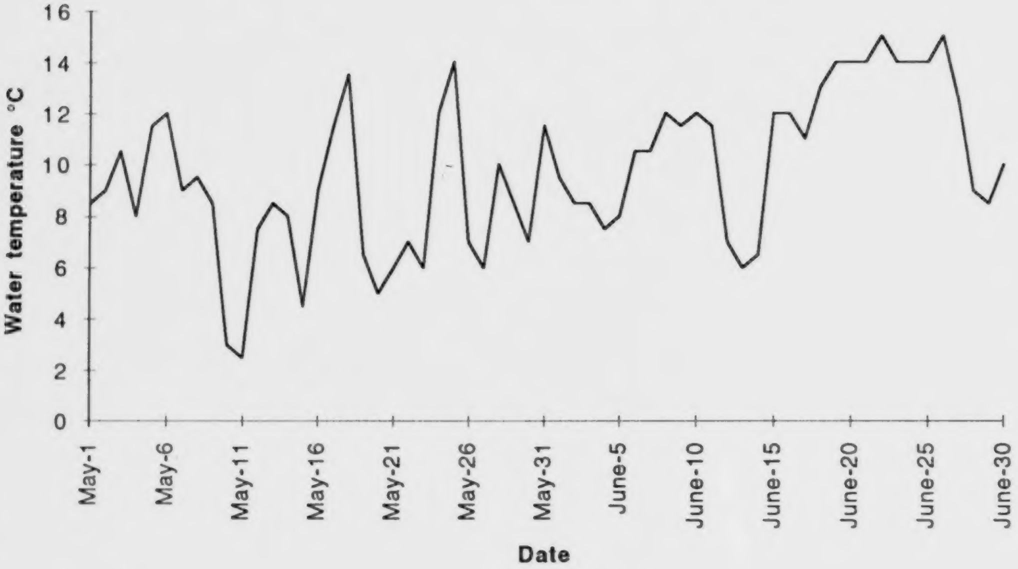

Figure 2-3. Maximum daily water temperatures in the North Ram River, Alberta as measured by a Ryan recording thermograph, May-June, 1992.

however, the majority of the fish (6 of 8 trout) moved downstream to spawning areas.

Also, unlike fish in the North Ram River, most (5 of 8) implanted fish moved over 1 km from their site of capture to spawning areas. The mean distance of pre-spawning movements was 2.8 km (median 2.2 km; maximum 6.6 km). The distance moved to spawning areas by fish in Onion Creek, however, was not significantly ($N=17$; $P>0.05$) different from distances moved by fish in the North Ram River (mean 3.0 km, median 0.9, maximum 8.4 km).

Although pre-spawning movements of fish in Onion Creek did not differ from movements of all fish in the North Ram River combined, fish in Onion Creek did make significantly shorter ($N=12$; $P\leq 0.05$) pre-spawning movements than fish that spawned in the tributaries of the North Ram River. The distance of pre-spawning movements of fish in Onion Creek, however, did not significantly differ ($N=13$; $P>0.05$) from fish that spawned in the mainstem and side-channels of the North Ram River.

Distances moved to spawning areas did not significantly differ ($N=17$; $P>0.05$) by sex when data for all fish (North Ram River and Onion Creek) were combined, or in the North Ram River ($N=9$; $P=0.05$). In Onion Creek, however, females ($N=2$) did make significantly ($N=8$; $P<0.05$) longer moves than males ($N=6$).

Spawning

North Ram River

Spawning of implanted fish occurred from June 3 to June 9 in 1991 (one fish) and from May 4 to June 14, in 1992 (17 fish). The first fish to spawn in 1992 (a female) was observed digging a redd when the water temperature was 5° C. Since the fish were located every other day, some (5 of 9 in 1992) of the fish were not observed spawning. Fish were also wary during spawning and would quickly move to cover when approached. In most instances, redds were seen near the locations of spawning fish. When redds were found in the area and other fish closely accompanied the implanted fish, I suspected spawning was occurring.

Fish that moved into tributaries to spawn stayed in the tributaries from 2 to 19 days. The duration of the stay did not differ by sex. Two fish moved into Cripple Creek, one male stayed 16 days and one female stayed 1-3 days. One male fish moved into Nice Creek in 1991, and two (1 male, 1 female) in 1992. In 1991, one trout was captured in an upstream trap near the mouth of Nice Creek and implanted with a radiotransmitter. During the 12 days it spent in Nice Creek, the male was seen spawning on three different redds. In 1992, one female stayed in Nice Creek 15 days, and one male moved into Nice Creek where it was located under cover for 5 days before it left.

In both drainages and in both years, fish showed a common pattern of movement during spawning. Fish moved frequently but stayed within a small area (approx. 400 m) that included several spawning sites.

Onion Creek

Spawning of radio-tagged fish in Onion Creek was first observed on May 12 and lasted until June 10. The water temperature was 6.5°C when the first fish was observed spawning. Although the mean date when fish first spawned in the North Ram River was five days earlier than those in Onion Creek, there was no significant difference ($N=16$; $P>0.05$) between the two drainages of the time when individuals were first observed or suspected spawning. Similarly, throughout the Ram drainage, the date when fish were first observed spawning was not significantly correlated ($N=16$; $P>0.05$) with altitude. Throughout the drainage, there was also no relationship between date of first spawning and weight of fish ($N=16$; $P>0.05$).

Post-spawning Movements

North Ram River

During 1991 and 1992, distinct post-spawning movements were common among implanted fish in the North Ram River. After spawning, most (7 of 9) fish moved more than 1.0 km from spawning areas. The mean post-spawning distance moved was 5.2 km (median 4.1 km, maximum 10.9 km). Most (7 of 9) of these fish moved downstream after spawning, but two fish moved upstream 0.6 - 2.0 km.

The post-spawning movements of fish that spawned in tributary streams were significantly longer (N=9; $P<0.05$) than those of fish that spawned in the mainstem or side-channels of the North Ram River. Trout that spawned in the mainstem or side-channels (N=5) made mean post-spawning movements of 2.7 km (median 2.0 km, maximum 6.4 km) while trout that spawned in tributaries (N=4) made mean post-spawning movements of 8.4 km (median 10.0 km, maximum 10.9 km).

In both drainages, after fish finished their post-spawning movements, they all stayed within a 400 m area until observations were ended June 28 (2.5 - 7 weeks). Most fish (6 of 7 fish) occupied 3 or fewer locations in the last half of June.

Onion Creek

Unlike trout in the North Ram River, only 1 of 8 implanted spawners in Onion Creek made downstream post-spawning movements. This fish was a post-spawning mortality. Of the 7 remaining fish, 4 moved less than 1 km from their spawning sites and 3 fish moved 2.4 - 2.5 km upstream.

In Onion Creek, post-spawning movements of fish were significantly shorter (N=17; $P<0.05$) than those of fish in the North Ram River. The mean post-spawning distance moved in Onion Creek was 1.2 km (median 1.1 km), while the mean was 5.2 km (median 4.1 km) in the North Ram River. The maximum distance moved by an individual in Onion Creek (2.5 km) was also shorter than the maximum in the North Ram River (10.9 km). Although fish in Onion Creek made shorter post-spawning movements than those in the North Ram River, post-spawning movements of fish in Onion Creek were not significantly different ($N=13$; $P>0.05$) from fish that spawned in the mainstem or side channels of the North Ram River. Post-spawning movements of fish in Onion Creek were, however, significantly ($N=12$; $P<0.05$) shorter those of fish that spawned in tributaries of the North Ram River.

Post-spawning movements did not significantly differ ($N=17$; $P>0.05$) by sex when data for all fish (North Ram River and Onion Creek) were combined. Post-spawning movements also did not differ by sex for fish in the North Ram River ($N=9$; $P>0.05$) or Onion Creek ($N=8$; $P>0.05$) when analyzed separately.

Post-spawning Mortality

During the study, 3 of 23 implanted trout died after spawning. One, a male which spent 16 days in Cripple Creek, was found dead 8 days after leaving the spawning stream. Another post-spawning mortality was a female which spent 14 days spawning in the North Ram River and its sidechannels near Nice Creek. It was found dead 22 days after spawning. The other post-spawning mortality was a female which was found dead 31 days after it was suspected to have spawned, this fish was eaten by a predator. These fish were monitored for 34-58 days after their release before being found dead.

Predation

Two fish were found dead shortly after implantation, and are suspected of being killed by predators. One of the fish that was confirmed dead is suspected of being caught by an angler, another fish that was lost is suspected of being preyed upon by a merganser. This was a 268 mm (FL) and 202 g fish.

Discussion

It was common for radiotagged cutthroat trout in both drainages to move downstream to spawn. This occurred despite the availability of spawning habitat upstream. In the North Ram drainage, both of the fish that were tagged upstream of Cripple Creek made initial downstream spawning movements. Once fish reached the mouths of Nice Creek or Cripple Creek they moved upstream into them to spawn. I hypothesized that these fish would move upstream to spawn in Joyce River, which has historically been heavily used for spawning (Allan 1978). Most (75 %) of the fish from Onion Creek also moved downstream to spawn. These patterns are contradictory to the upstream pre-spawning movements observed by many researchers (Cope 1956, Bjornn and Mallet 1964, Allan 1978, Shepard *et al.* 1984) and brings up the interesting question of what is guiding the fish to their spawning areas. It is unlikely that these fish are using olfaction to home to spawning areas as Groves *et al.* (1968) suggests, unless they have adapted to first move downstream of their home stream or spawning area before keying in on their olfactory cues. The movement of fish downstream to spawning areas may be related to the availability of overwintering habitat. If overwintering habitat is limited in lower portions of river systems, the fish would be forced to overwinter farther upstream, especially in systems like the Ram where downstream migrations are limited by waterfalls. The fish would then need to move downstream to gain access to spawning areas in the lower parts of the river system.

The cutthroat trout in the North Ram River and Onion Creek differed in their patterns of pre-spawning movement. The cutthroat trout in Onion Creek spawned in the same stream where they spend their entire lives, despite being able to move downstream and spawn in the rest of the Hummingbird drainage. This is characteristic of a resident or fluvial life history pattern (Likness and

Graham 1988; Varley and Gresswell 1988). In the North Ram River, some of the fish spawned in the mainstem and side-channels of the river and moved short distances to spawning areas, these are resident characteristics. Other fish moved over 8 km from the North Ram River to spawn in tributary streams, these are characteristics of a migratory life history pattern (Likness and Graham 1988; Varley and Gresswell 1988). The significant difference in the distances moved to spawning areas, between tributary spawners and fish that spawned in mainstem and side-channels of the North Ram River, suggests that there are two distinct groups of fish with separate behavioural strategies. The lack of a significant difference between movements of the resident spawners in the North Ram River, and Onion Creek spawners suggests that these two groups both exhibit similar resident spawning strategies. The similarities in these two groups are also strengthened by the significant difference in the distance of pre-spawning movements between the resident Onion Creek spawners and fish that spawned in the tributaries of the North Ram River. Thus, in the North Ram River, there appear to be two groups of trout with the same overwintering and summer habitat which exhibit different strategies for spawning. Other researchers have found both resident and migratory life history types in the same drainage (Johnson 1963) but there are no documented cases of these two types living in the same river section.

I suggest that despite the differences in life history type, there are no genetic differences between the groups. This is because the fish were stocked in the stream, at the earliest, in 1955. In the few generations that occurred in the short amount of time the fish were present in the Ram system, it is unlikely that they developed different spawning strategies, especially since they probably originated from lacustrine populations.

Pre-spawning movements were affected by water temperature (Figure 2-3). Fish made significantly longer moves during periods of above average water temperature. They did not, however, make significantly more movements during periods of high water temperature. Thus, although the fish made just as many moves when it was colder, more long moves were made when it was warmer. Since fish are poikilotherms, one would expect them to make longer movements when metabolic rates are at higher levels, while not being restricted in making smaller movements under colder conditions. Since fish can swim faster at higher water temperatures (Sullivan 1953, Brett 1958) one would also expect that they would make longer movements at this time. Other researchers have observed that pre-spawning movements are halted by abnormally low (0°C) water temperatures (Cope 1956), but did not relate movements to mean water temperatures. I did not relate pre-spawning movements to abnormally low water temperatures since it would require a subjective statement of when water temperatures were abnormally low. I also could not relate pre-spawning movements to near freezing temperatures since maximum daily water temperatures were not observed below 2.0°C during the study period (Figure 2-3).

Significantly fewer pre-spawning movements occurred when discharge fluctuated above the mean between locations of fish. This indicates that fish make more pre-spawning movements when water discharge is more stable. Fish may move more at this time because of lower turbidity or water velocity, allowing fish to conserve energy. Many researchers have suggested that initial spawning movements of spring spawning trout are stimulated by increased flows (Rayner 1942, Johnson 1963, Allan 1978) but there have been few observations on how water discharge affects later pre-spawning movements. One researcher, however, found that cutthroat trout in one creek moved upstream to spawning areas during the evening and night (Cope 1956). Cope (1956) hypothesized that the trout were stimulated to move upstream at night by increased water discharge from the previous afternoons melt. This pattern, however, is not supported by our research and may be a unique situation characteristic of a small tributary stream where increased flows are necessary to allow access to shallower areas.

Distances moved to spawning areas did not differ by sex in the North Ram River, or when the North Ram River and Onion Creek data were combined. Thus neither males nor females moved from farther parts of the drainage to spawn with fish that overwintered closer to spawning areas. The significantly longer moves made by females versus males in Onion Creek likely were due to the low number of implanted females (2 of 8) in the drainage that were still alive at the time of spawning. The statistical significance found in this test probably does not reflect a biological significance.

Initial spawning in the two drainages occurred at roughly the same time and temperature (5.0-6.5°C). Cutthroat trout were noted first spawning at 6°C in the North Ram River by Allan (1978), while other researchers state that cutthroat trout spawn at water temperatures ranging from 5.5°C to 15.5°C (Varley and Gresswell 1988).

The date when fish spawned in the Ram Drainage (1250 m - 2100 m) was not significantly related to elevation. Varley and Gresswell (1988) however, have suggested that the spawning migrations are affected by elevation. They cited their own and other's research (Platts 1959) as having a trend of peak migration being successively later (varying from mid-March to late July) as altitudes increased (from 1829 m to 2565 m, a range of 736 m). However, since I found no significant difference in dates of spawning initiation over an altitude range of 850 m, it is unlikely that spawning migrations are affected by altitude, but by water temperature, which would commonly change with altitude. There was, however, little difference in water temperature with altitude between the Onion and North Ram drainages, this is probably because of differences in riparian zones. Although Onion Creek is at a higher elevation (1700-2100 m) water temperatures are as warm as in the North Ram River (elevation 1250-1600m) possibly because Onion Creek receives more solar radiation. Onion Creek runs through a wide, shallow valley and is surrounded by bushes and few trees, allowing the sunlight to warm the water, the North Ram River, however, is surrounded by mature spruce and pine, and runs through a deep valley, along large hills. The trees and hills both shade the stream from the sun during much of the day. Onion Creek is largely influenced by goundwater input which also likely makes the stream warmer earlier in the spring.

The pattern of movement I observed during spawning has not been previously reported. The fish appeared to have a small territory (approximately 400 m reach) during spawning. The females made redds within the territory, and the males attended several redds within their spawning areas, perhaps attempting to spawn with all females in their territory. Similarly, Smith (1941) observed female cutthroat trout making 5-6 redds within a 1.5 m length of stream, however, these fish were confined to small stretches of an experimental stream.

Similar to pre-spawning movements, the pattern of post-spawning movements differed between the North Ram River and Onion Creek. After spawning, most radiotagged fish in the North Ram river moved downstream, while in Onion Creek, most of the fish that made post-spawning movements, moved upstream. I hypothesized that trout would move downstream after spawning. I expected downstream post-spawning movements since salmonids commonly move upstream to spawn instead of downstream, and move downstream after spawning, instead of upstream (Varley and Gresswell 1988). I also expected downstream post-spawning movement since spawning causes a loss of body condition (Mottley 1938) and making upstream movements against the current would result in more energy expenditure and loss of condition than moving downstream, thus increasing the likelihood of mortality.

Similar to the pre-spawning movements I found two patterns of post-spawning movements, one, of fish migrating from spawning locations in tributaries back to the main river (migratory life history type), and one, of fish not moving out of the river or stream where they spawned (resident life history type). Similar to pre-spawning movements there are no documented cases of these two life history types occurring in the same river section.

There is a possible explanation why downstream pre-spawning and upstream post-spawning movements have not been recorded in riverine systems. Fisheries managers often only install traps that will catch fish as they move upstream to spawning areas (Platts 1959, Johnson 1963, Huston 1973). Most, if not all, don't consider the possibility that fish could exhibit alternate behaviour. Thus, the pattern may be common, but just has not been properly looked for.

Cutthroat trout appear to display a good deal of plasticity in the patterns of movements associated with spawning. The diverse patterns of spawning movements that I observed are similar to those found in some lake resident spring spawning salmonids. In Loon Lake, British Columbia, most rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) move upstream to spawn in the inlet stream, and made post-spawning movements back down into the lake (Lindsey *et al.* 1959). This pattern is similar to that exhibited by most fish in the North Ram River. In Loon Lake, some of the fish move downstream out of the lake and spawn in the outlet stream (Lindsey *et al.* 1959). This pattern is similar to that which most of the fish in Onion Creek exhibit. Also in the Loon Lake system, there is a third group of fish that move down into the outlet stream and then move upstream into a tributary of the outlet to spawn (Lindsey *et al.* 1959). This pattern is similar to that exhibited by two fish in the North Ram River which moved downstream and then moved up into Cripple or Nice Creek to spawn.

The distance fish moved after spawning may rely on several factors. Since many of the fish spawn and reside all year in the same reach of stream, in both Onion Creek and North Ram River, one would expect the distances moved to spawn would be small. In these resident fish, the distance moved after spawning should not be related to the distance moved to spawning areas. The distance moved to spawning areas may merely be a function of how far suitable spawning habitat is from suitable overwintering areas. If a fish could overwinter and spawn within the same section of stream, little pre-spawning movement would likely occur. Similarly, when suitable summer habitat is in the vicinity of spawning habitat, there may be no post-spawning movements, similar to the findings of Miller (1957). Hence, post-spawning movements of resident fish should be determined by availability of habitat, dominance of fish, and variance of individual behaviour.

The relationship between spawning mortality and the time a spawning fish spends in a tributary has been well studied (Platts 1959; Ball and Cope 1961; Huston *et al.* 1984, Jones *et al.* 1985). Of the three radiotagged fish that died following spawning, two were tributary spawners, one of which was a male that spent 16 days in a tributary stream. Unlike this male, the one female, which spent 16 days in a tributary, did not die after spawning. Although the fish spent the same amount of time in the tributary streams, the male died and the female did not. Other researchers have found that spawning mortality in trout is lower in females than males (Hartman 1962). This is probably due to the higher rate of weight loss which males incur during spawning (Mottley 1938), and the high rate of competition between males during spawning (Hartman 1957).

The spawning mortality that I observed is similar to that reported by other researchers. I found spawning mortality of radiotagged cutthroat trout to be 13.6 % (3 out of 22 fish implanted in 1992) while Jones *et al.* (1985) found spawning mortality of cutthroat trout at a rate of 12.9 %. Other researchers have found the rates of spawning mortality for cutthroat trout to be much higher, 27 % - 60 % (Platts 1959; Ball and Cope 1961; Huston *et al.* 1984). Similarly, post-spawning mortality rates for rainbow trout have been found to range from 43 % to 86 % (Hartman *et al.* 1962). The relatively low spawning mortality that I observed may be due to shorter migrations to spawning areas made by fish in the Ram system compared to trout studied by other authors.

Cutthroat trout in the Ram River exhibited a pattern of movement associated with spawning that has not previously been described. The fish changed from a sedentary life style in a very localized area during late winter, to one characterized by sudden movement to spawning areas. Once at spawning areas, the fish made a large number of small movements, while staying in a small reach of stream. After spawning, the fish again made a sudden movement to their summer habitat, where they made little if any subsequent movement.

These findings make it clear that trout make a variety of spawning movements, and that spawning habitat, not only in tributaries but also in the mainstem and sidechannels of rivers, needs to be protected. Our results show that fish in a river may not all conform to one pattern of spawning movements, thus, research on tributary spawners, or trout making more common types of movements may not represent that of the whole population.

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Chapter Three

Fall and winter ecology of cutthroat trout in the Ram River, Alberta

Introduction

In areas with average winter air temperatures below 0.0°C, ice formation and flow reduction severely decreases the amount of available overwintering habitat for salmonids in mountain streams (Chisholm *et al.* 1987). Overwintering strategies of salmonids may be markedly influenced by severity of climate and habitat availability, however, little research has been done in this area.

The choice of overwintering habitat and the distance moved to overwintering habitat can be influenced by climate and the effects of ice formation on habitat availability. Hunt (1974) noted a decrease in fall emigration of brook trout (*Salvelinus fontinalis* (Mitchill, 1814)) after pool area and cover were increased by a habitat improvement project. In areas with severe winter conditions, available winter habitat may be drastically decreased by ice exclusion (Chisholm *et al.* 1987), forcing trout to migrate long distances to find suitable ice free habitat. Thus, in some systems, to avoid winter dangers, trout make long migrations to suitable overwintering habitat. Extensive migrations (up to 101 km by a cutthroat trout) to overwintering areas have been documented by Bjornn and Mallet (1964). Conversely, in other systems, trout may find suitable habitat in the same section of stream where they reside the rest of the year. In a coastal British Columbia stream, a majority of cutthroat trout stayed within a 22 m^2 home range throughout the year (Heggenes *et al.* 1991a). Similarly, in a Wyoming stream, brook trout moved less than 500 m from fall to winter habitat (Chisholm *et al.* 1987). The use of a small home range in all seasons by cutthroat trout was also suggested by Miller (1954, 1957).

Reduction in availability of suitable habitat can expose trout to winter conditions which cause mortality. Most winter mortality is linked to ice and snow conditions (Reimer 1957, Needham and Jones 1959), however, studies of this issue are sparse and not thorough. Ice and snow cause mortality of stream dwelling fish in several ways. Mortality has been documented from the presence of frazil ice, stream dewatering created by ice damming, and collapsing snow banks. Needham and Slater (1944) found several hundred dead trout beneath a collapsed snow bank. They also noted several smaller losses of this type. Winter mortalities are also caused by frazil ice. Frazil ice forms when turbulent water that is already at 0.0°C, loses further heat to the atmosphere (Ettema *et al.* 1982). When the water temperature dips below 0.0°C the water is termed 'supercooled' (Tsang 1982). While the water is supercooled, small (0.1-5.0 mm) disc or needle shaped ice crystals, known as frazil ice, form in the water column (Osterkamp and Gosink 1982). These ice crystals can plug the mouths and gills of trout, causing mortality (Tack 1938). While the water is supercooled, frazil crystals are more likely to be adhesive (Carstens 1966), sticking to each other, to the substrate, and to underwater objects (Osterkamp and Gosink 1982, Tsang 1982). The buildup of frazil ice forms a thick, spongy coating of anchor ice on underwater debris; this is the most common way anchor ice is formed (Tsang 1982). Anchor ice can grow to such an extent that it dams rivers and streams. Ice dams of this type can lead to large fluctuations in water depths (Maciolek and Needham 1952). While water depth increases upstream of the dam, it decreases below the dam. On one January day, Maciolek and Needham (1952) found 63 trout lying on the rocks in dewatered pools below an ice dam. They also noted several other instances of this type.

Winter ecology of trout has been studied in several areas, but little research has been conducted where winters are severe and frazil or anchor ice occur. Cunjak and Power (1986) studied winter trout ecology in three Southern Ontario streams. Anchor ice was occasionally seen in two of these streams. By snorkeling in open water reaches, they found that 86 % of the brook and brown trout (*Salmo trutta* (Linnaeus, 1758)) they observed were in large aggregations and most of the aggregations were found in locations where groundwater discharge maintained water temperatures 2.0°-6.0° warmer than the rest of the stream. Another study of trout ecology where harsh winter conditions occurred was conducted by Chisholm *et al.* (1987). They observed stream conditions at various altitudes and found many differences in ice formation which were correlated with altitude. They observed extensive surface ice in stream stretches below 2550 m, but found little surface ice above 2900 m because snow bridged the streams. They stated that the stream reaches between 2550 m and 2900 m experienced the harshest conditions, including anchor ice. Chisholm *et al.* (1987), however, only studied trout that resided above 2990 m and were not exposed to the harshest winter conditions which include anchor ice. The trout all used low water velocities and abundant cover in the low (<1.5 %) gradient stream stretches where they were tagged.

While trout have been studied in a few areas where severe winter conditions occur, the trout in these studies were all in low gradient areas and no direct effects of frazil or anchor ice were mentioned. I designed a study to evaluate habitat use by trout in low, mid, and high altitudes of a river system where a variety of ice conditions exist. I also studied trout in both low and high gradient streams. The study was designed to evaluate the relationship between movement and habitat use, and to determine how trout react to frazil and anchor ice development. To accomplish these goals, I used radiotelemetry so I could track individuals through changing environmental conditions.

Considering the results of Cunjak and Power (1986) and Chisholm *et al.* (1987) I hypothesized that trout would use large deep pools with abundant subsurface cover, and that the pools themselves would be covered by surface ice or snow bridging. I hypothesized that, when available, trout would gather in areas of warm water discharge. I also hypothesized that trout would have to move long distances to find these kinds of habitats.

Study Area

This study was conducted in the Ram River drainage located in west central Alberta (52° 00'-52° 20' N latitude, 116° 20'-115° 35' W longitude). The system (Figure 3-1) originates in the Ram Mountain Range and flows easterly towards the town of Rocky Mountain House. Within the Ram River drainage, work was focused on the North Ram River (elevation 1250-1600 m; latitude 52° 14' - 52° 19' N, longitude 115° 40' - 116° 03' W), Hummingbird Creek (tributary of the Ram River, elevation 1700-2100 m; latitude 52° 03' - 52° 08' N, longitude 115° 55' - 116° 10' W) and its tributary Onion Creek. Access from downstream to both Hummingbird (including Onion) and the North Ram systems are restricted by waterfalls (Figure 3-1). These waterfalls restrict fish from making long migrations downstream and isolate the two systems from each other.

The flow regimes differ between Hummingbird Creek and the North Ram River drainages. The North Ram River is a high gradient river (average 10.9 m /km) and has highly fluctuating water flows (Figure 3-2) due to its high gradient and because its major source is from surface runoff. Due to frequent fluctuations in water level, the quality of trout habitat also frequently changes in both a spatial and a temporal sense. This is not so in Onion Creek. Although most of the Hummingbird Creek drainage is high gradient, Onion Creek is not. Onion Creek is low gradient (average 8.1 m/km), surrounded and fed by muskeg (fen). It is primarily spring fed and has a very stable flow regime, unlike the rest of the Hummingbird drainage. Onion Creek is also more meandering than the North Ram River, having a sinuosity index of 1.6 while the North Ram River has a sinuosity index of 1.3. Within the study area, the degree of sinuosity decreases in both drainages as the stream or river gets closer to its mouth.

Winters in the Ram River drainage are characterized by moderate snowfalls (126-236 cm; 1980-89 (measured at the Environment Canada

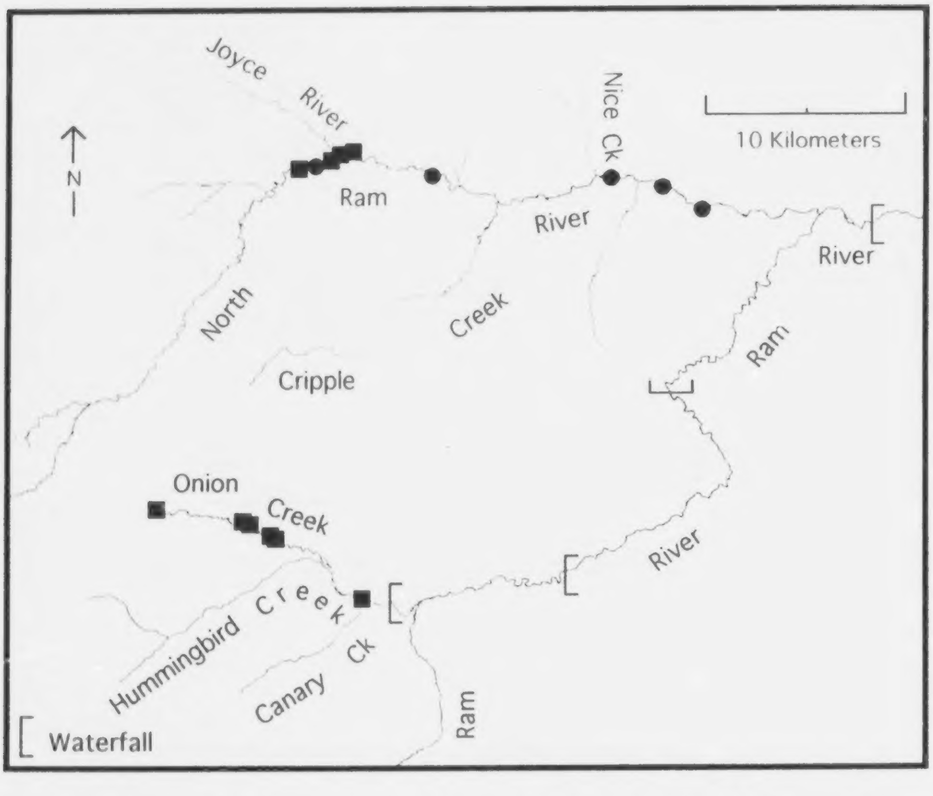
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Figure 3-1. Map of the Ram River drainage (latitude, 52° 07' N - 52° 15' N; longitude, 116° 14' W - 115° 37' W; elevation 2100 m - 1250 m). Release points of radio-tagged cutthroat trout are shown (as solid squares for 1991, 22 fish; as solid circles for 1992; 23 fish) in Onion Creek and the North Ram drainage, Alberta. Fish were tracked Aug.-Nov. 1991 and Oct.-Dec. 1992.

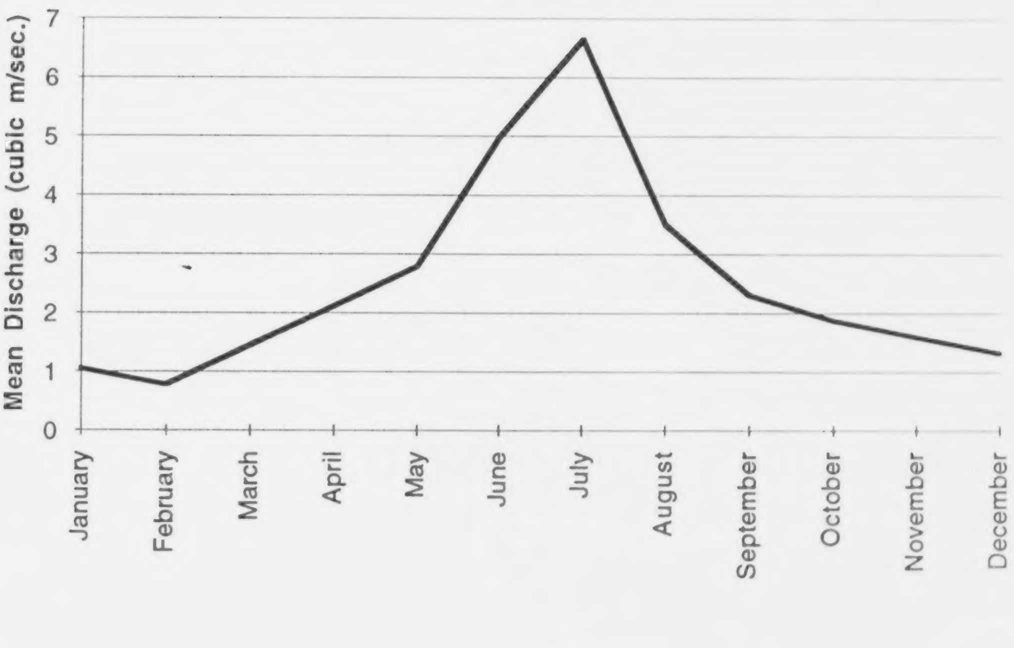


Figure 3-2. Mean monthly water discharge (m3/s) in the North Ram River as measured by the Environment Canada water gauging station No. 05DC011 located in the study section. The average of monthly means were calculated from 1981-1990 historical data from the gauging station. Flows for November - April were estimated using staff gauge measurements and were extrapolated from the linear relationship between staff gauge measurements and discharge recorded at the gauging station.

Weather Station, in Nordegg, 30 km north of the study area), low temperatures (Figure 3-3), and decreased water discharge in most areas (Figure 3-2). Mean monthly air temperatures for fall and early winter are shown in Figure 3-3. Surface ice formation in the drainage usually starts in late October to early November, and the minimum water temperature of 0.0°C is also reached at that time.

Methods

Movements of cutthroat trout were monitored using radiotelemetry. In 1991, 22 cutthroat trout (243-362 mm total length, TL) were implanted with radiotransmitters (Table 3-1); they were captured by angling and electroshocking in August and September. Eleven fish were obtained between Aug. 18 and 29 from four reaches of the North Ram River (Figure 3-1). Between Aug. 15 and Sept. 17, eleven fish were obtained from four reaches of Onion Creek, and one reach in Hummingbird Creek (Figure 3-1). The trout were located at least three times a week until October 28, and several trout were again located on Nov. 3, 11, and 17. In 1992, movements were only studied in the North Ram River. Twenty-three cutthroat trout (246-475 mm TL) were implanted with radiotransmitters (Table 3-2). They were captured by angling from three reaches in the North Ram River (Figure 3-1) from Oct. 2 to Oct. 31 and each fish was located at least three times a week until Dec. 21. Several fish were tagged in spring 1992, to study spawning movements, the transmitter in one of these fish was operational throughout the fall-winter study period. This trout was captured by electroshocking and implanted on April 28, 1992.

Trout were implanted in 3-4 reaches (Figure 3-1) of the North Ram and Hummingbird drainages so that a variety of movements were possible. I hypothesized that fish tagged in upper and middle reaches would move

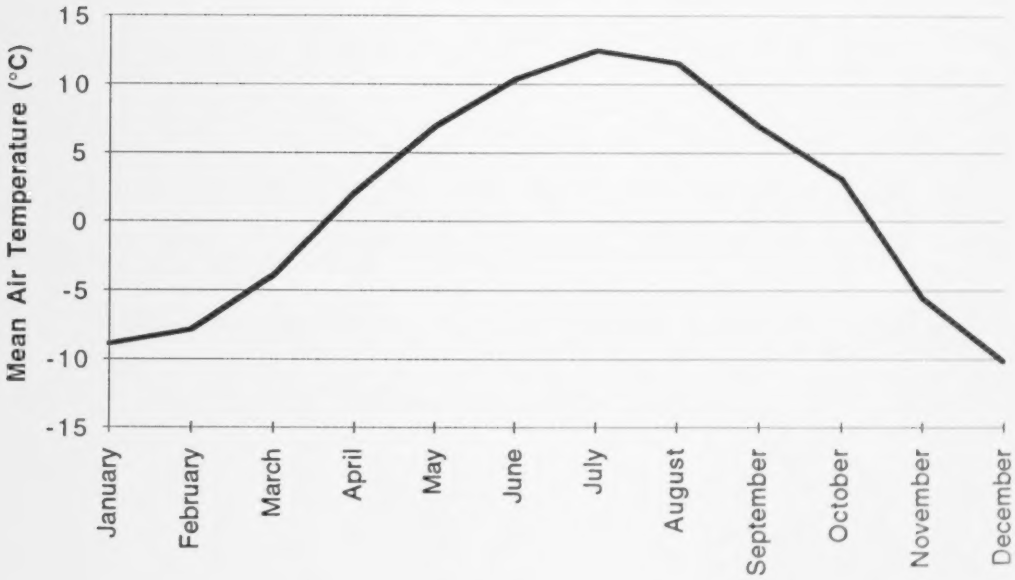


Figure 3-3. Mean monthly air temperature (°C) in the Ram River area as recorded from 1980-1989 data from Environment Canada weather stations at Ram Falls (10 km east of the study area) and Nordegg (30 km north of the study area).

Table 3-1. Length, weight, and release sites of radiotagged cutthroat trout from the North Ram River and Onion Creek, fall 1991. The KM tagged column indicates the kilometer above the confluence with the South Ram River for fish in the North Ram River, and kilometer above the confluence with Hummingbird Creek for fish in Onion Creek, the two trout implanted in Hummingbird Creek (H2) were captured at it's confluence with Canary Creek.

Fish #	Date Implanted	KM Tagged	Length (FL mm)	Weight (g)
1	Aug. 28/91	NR 29	362	600
2	Aug. 18/91	NR 29	264	232
3	Aug. 29/91	NR 30	248	184
4	Aug. 29/91	NR 31	264	210
5	Aug. 29/91	NR 31	334	416
6	Aug. 29/91	NR 31	285	332
7	Aug. 29/91	NR 31	292	286
8	Aug. 18/91	NR 31	254	184
9	Aug. 29/91	NR 33	304	322
10	Aug. 29/91	NR 33	319	336
11	Aug. 29/91	NR 33	333	430
12	Sept. 1/91	H 2	269	286
13	Sept. 1/91	H 2	254	198
14	Sept. 1/91	ON 5	256	180
15	Sept. 1/91	ON 5	243	152
16	Sept. 1/91	ON 7	244	164
17	Sept. 17/91	ON 7	253	157
18	Sept. 1/91	ON 8	264	200
19	Aug. 15/91	ON 15	260	186
20	Aug. 15/91	ON 15	255	214
21	Aug. 15/91	ON 15	257	184
22	Aug. 15/91	ON 15	314	310

Table 3-2. Length, weight, and release sites of radiotagged cutthroat trout from the North Ram River, fall 1992. The KM tagged column indicates the kilometer above the confluence with the South Ram River.

Fish #	Date Implanted	KM Tagged	Length (FL mm)	Weight (g)
23	Oct. 26/92	NR 7	352	558
24	Oct. 26/92	NR 7	445	1040
25	Oct. 2/92	NR 8	475	1180
26	Oct. 2/92	NR 9	400	866
27	Oct. 26/92	NR 10	305	382
28	Apr. 28/92	NR 12	410	938
29	Oct. 2/92	NR 25	307	334
30	Oct. 2/92	NR 25	296	268
31	Oct. 2/92	NR 25	249	166
32	Oct. 5/92	NR 25	326	422
33	Oct. 2/92	NR 25	254	166
34	Oct. 2/92	NR 25	261	202
35	Oct. 2/92	NR 25	270	220
36	Oct. 5/92	NR 25	394	726
37	Oct. 5/92	NR 25	317	348
38	Oct. 5/92	NR 25	327	430
39	Oct. 3/92	NR 32	246	166
40	Oct. 3/92	NR 32	271	214
41	Oct. 3/92	NR 32	288	264
42	Oct. 3/92	NR 32	360	548
43	Oct. 3/92	NR 32	270	202
44	Oct. 3/92	NR 32	279	198
45	Oct. 31/92	NR 32	322	382

downstream to overwinter. Fish were also tagged in lower and middle reaches to test whether trout would move upstream to overwintering areas.

After capture, fish were anaesthetized with a 200 mg/liter solution of tricaine methane sulfonate (MS-222) (Bidgood 1980) and transmitters were inserted into the body cavity (details given in chapter 2).

Two types of transmitters were used to monitor fish movements. The first type weighed three grams in air (1.8 g in water) and had a predicted life of 50 days (Model 393 transmitters Advanced Telemetry Systems Inc., Isante, Minnesota). The second type weighed 3.5 grams in air (2.1 g in water) and had a predicted life of 110 days (Model 357 transmitters Advanced Telemetry Systems Inc.). The smaller transmitters were used in smaller fish to maintain a low transmitter weight to body weight ratio. The transmitters emitted 54-63 pulses per minute, each transmitting on a unique frequency in the range of 150.000 - 150.160 MHz. A Fieldmaster radio receiver (Advance Telemetry Systems Inc.) was used to monitor the transmissions. Fish locations were fixed with a three element YAGI antenna and recorded on aerial photographs (scale 1:5000 or 1:3750). The accuracy of the locating method was frequently checked by visually finding the fish and was estimated at 0.5 m, similar to Chisholm *et al.* (1987). When the location of the implanted fish were recorded on the aerial photographs, however, the accuracy decreased from 0.5 m to approximately 5 m. Therefore, a fish was not considered to have moved unless the two locations differed by 5 m.

Habitat use data were obtained by noting the location of radiotagged cutthroat trout during daylight. The 1 m^2 area at the location of the fish was assumed to be the habitat it was using. Habitat data were recorded at the fish's location, including macrohabitat type (pool, run, riffle), substrate type, water depth, and cover type. Water depth was recorded by direct measurement with a calibrated rod, and streambed material size was classified according to a modified Wentworth scale (Table 3-3) (Cummins 1962) similar to Bain *et al.* 1985.

Habitat availability data were obtained in the reaches where tagged fish were found using stratified random sampling (Baltz *et al.* 1991). Data were collected in the sections of the North Ram River (10 km), Hummingbird (1 km) and Onion (8 km) Creeks where habitat use data were collected (Baltz *et al.* 1991). Five kilometers of the North Ram River were sampled in November 1991 and the remainder of the habitat availability sampling was done in November and December 1992. Sampling points (50 per km) were generated by selecting 4 digit numbers from a random numbers table. The first three digits signified distance in meters from the start of the stream kilometer, while the fourth number signified the proportion across the stream. A number of 6485 corresponded to a location 648 m upstream from the start of the stream kilometer and 5/10 the distance across the stream (Baltz *et al.* 1991). I alternated the side of the stream from which the distance across was measured. At the randomly selected point, habitat data were gathered in a 1 m^2 area, similar to radiotelemetry locations.

Habitat use may be influenced by the habitat available (Heggenes 1991b). To help remove this influence, I calculated preference values. Values of habitat preference (D) were calculated using methods of Heggenes *et al.* (1991b) first presented by Jacobs (1974):

$$D= \frac{r-p}{(r+p) - 2rp}$$

where r = proportion of resource used by the fish and p = proportion of the resource available in the environment. A preference value (D) of 0 indicates the

Table 3-3. A modified Wentworth substrate scale (Cummins 1962) used to classify stream substrate in the Ram River, Alberta, similar to Bain *et al.* 1985.

Substrate type	Size class (mm)	Code
Smooth Surfaces:		
Smooth bedrock		1
Sand, silt	<2	1
Small gravel	2-16	2
Large gravel	17-64	3
Small cobble	65-128	4
Large cobble	129-256	5
Boulder	>256	6

habitat is used in proportion with its availability, or no preference. Values ranging from -0.1 to -1.0 indicate the resource was used less than expected from its availability, and values ranging from +0.1 to 1.0 indicate the resource was used more than expected from its availability, or habitat preference (Heggenes *et al.* 1991b).

Data on habitat use of fish among dates and sites and data on direction of fish movement within sites were analyzed with a chi-squared test. Directional data, and proportions of fish moving between sites and years were analyzed with a chi-squared test. Depth data were checked for normality both in the raw form and when log transformed, when the data failed to meet the assumption of a normal distribution, Mann-Whitney U and Kruskal-Wallis tests were performed. To test whether grouped values for individual preferences indicated significant ($P<0.05$) preference Bonferroni family confidence intervals were calculated using the methods of (Neu *et al.* 1974) and (Byers *et al.* 1984). To test whether individual preferences varied by season or site, a value of 2 was added to the preference values (which varied from -1.0 to 1.0) so that they would all be positive, and they were compared using a Mann-Whitney U test since the data were not normally distributed. I also tested for correlations between preference values and in water depth and substrate roughness. This was done using a Spearman Rank Correlation since data were not normally distributed.

Results

Two Stage Habitat Use Pattern

Cutthroat trout in the Ram drainage exhibited a two-stage shift in habitat use from summer to winter. In August and early September, trout used a wide range of habitats including pools, riffles, and glides, but in the last half of September, many of the trout left the shallower habitats and aggregated in large pools. These pools were characterized by abundant woody debris (log jams and beaver caches), which was used as cover. Trout stayed in these pools until they were excluded from them by anchor ice. Since the trout aggregated in these pools and later moved to other areas to overwinter, I called these pools 'staging' pools. After anchor ice filled the staging pools, trout moved to overwintering areas less likely to be influenced by frazil and anchor ice. These overwintering areas included large deep pools with ice cover, or areas where water temperatures where higher than the rest of the stream due to ground water input.

Distance to Overwintering Areas

When moving to overwintering areas, trout made much shorter movements than I had hypothesized. The mean distance moved from release points to overwintering areas was 1.0 km (range 0.0-3.0 km; N=20) in 1991, and 2.4 km (range 0.0-7.6 km; N=17) in 1992. There was no significant difference (N=37; P>0.05) in the distances moved to overwintering areas between years.

Staging Pools

The first stage of movement from summer habitat to winter habitat was the move to staging pools. Five of twenty trout moved into staging pools from Sept. 17 to 21, 1991 (Table 3-4). Most (18 of 23) trout that were implanted with radiotransmitters in 1992 were captured in staging pools. The trout were in staging pools by October 2-3 when they were captured (Table 3-2).

Staging areas were deep and had abundant cover. The pools varied in depth from 0.65 to 1.77 m. Most staging pools (5 of 6) contained large amounts

Table 3-4. Direction and distance moved, and date of arrival at staging and overwintering areas for radiotagged cutthroat trout from the North Ram River and Onion Creek, fall 1991.

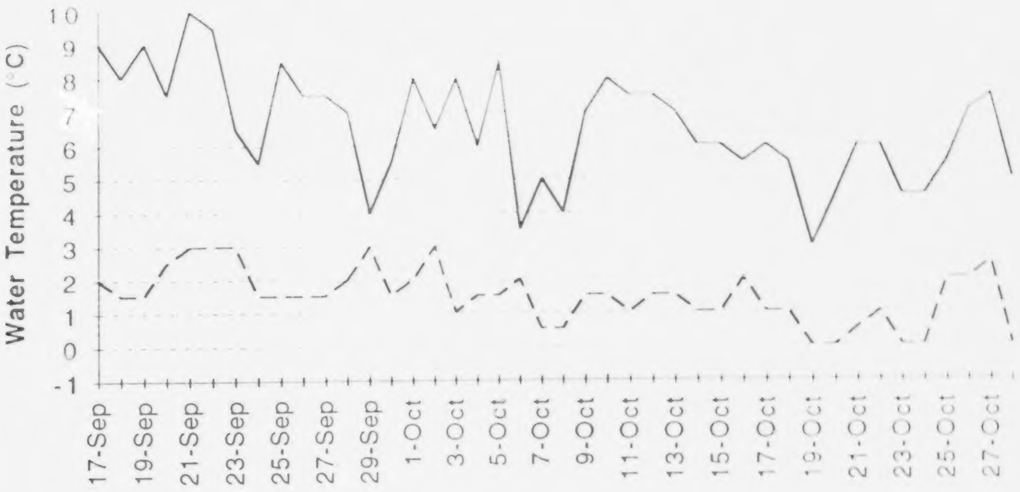
Fish	Site	Staging			Overwintering				Last
#		Dir.	Dist.	Date	Dir.	Dist.	Aggregating?	Date at	Location
1	NR 29				up	3.0	yes	Sept. 23	Nov. 17
2	NR 29								Aug. 18*
3	NR 30				none	0.0	yes	Oct. 26	Nov. 3
4	NR 31	up	1.1	Sept. 18	up	1.4	yes	Nov. 3	Nov. 3
5	NR 31	up	1.4	Sept. 18	up	0.6	yes	Nov. 17	Nov. 17
6	NR 31	up	1.1	Sept. 21	up	1.4	yes	Nov. 3	Nov. 10
7	NR 31				down	0.7		Sept. 23	Oct. 28
8	NR 31				up	0.2		Sept. 2	Oct. 28
9	NR 33				down	0.1		Sept. 18	Oct. 4#
10	NR 33				up	3.0		Sept. 16	Oct. 18*
11	NR 33				down	0.3	yes	Nov. 3	Nov. 17
12	H 2				down	0.2		Sept. 10	Nov. 14
13	H 2								Sept. 13+
14	ON 5				up	1.5		Sept. 8	Oct. 27
15	ON 5				up	0.2		Oct. 10	Oct. 27
16	ON 7	up	2.2	Sept. 17	up	0.3	yes	Oct. 17	Oct. 24
17	ON 7	up	2.2	Sept. 17	up	0.3	yes	Oct. 17	Oct. 24
18	ON 8				down	0.4		Oct. 27	Oct. 27
19	ON 15				down	0.5		Sept. 17	Oct. 24
20	ON 15				none	0.0		Sept. 17	Oct. 27
21	ON 15				down	3.1		Sept. 14	Oct. 24
22	ON 15				down	2.9		Sept. 10	Oct. 24

+Fish was caught by angler. * Fish was lost. # Fish lost to predation.

of woody debris for cover. The woody debris was composed of log jams and beaver caches. Although there were no beaver dams on the mainstem of the North Ram River, all of the staging pools in the North Ram drainage contained beaver caches. The woody debris in the staging pools was dense, providing cover from predators. The staging pool used by implanted fish in Onion Creek also had cover provided by undercut banks and overhanging vegetation.

The staging pools, however, were only used from September 17 to the end of November when fish were forced out by anchor ice accumulation on the woody debris. This exclusion was related to the production of frazil ice. During cold nights, frazil ice formed in some areas. It was first seen after minimum water temperatures reached 0.0°C. Water temperatures reached a minimum of 0.0°C on Oct. 28 (-20°C minimum air temperature), in 1991, and on November 1 (-8°C minimum air temperature), in 1992 (Figures 3-4 and 3-5). After frazil ice appeared, it adhered to objects in the water column and formed anchor ice on them. Anchor ice was first seen on Oct. 28, in 1991, and on Nov. 6 in 1992. Anchor ice coated the substrate of the streambed and engulfed woody debris that trout were using as cover. In early fall, the anchor ice melted with warming of water temperatures during the day (Figures 3-4), but as maximum water temperatures decreased to 0.0° C with the onset of winter, anchor ice accumulated in the water column. Anchor ice excluded fish from the staging pools, and filled much of the water column in other parts of the system. The movement of fish from staging pools to overwintering areas occurred from Oct. 17 to mid-November in 1991, and from October 12 to the end of November, in 1992 (Table 3-4 and 3-5).

Water Temperatures 1991



Water Temperatures 1992

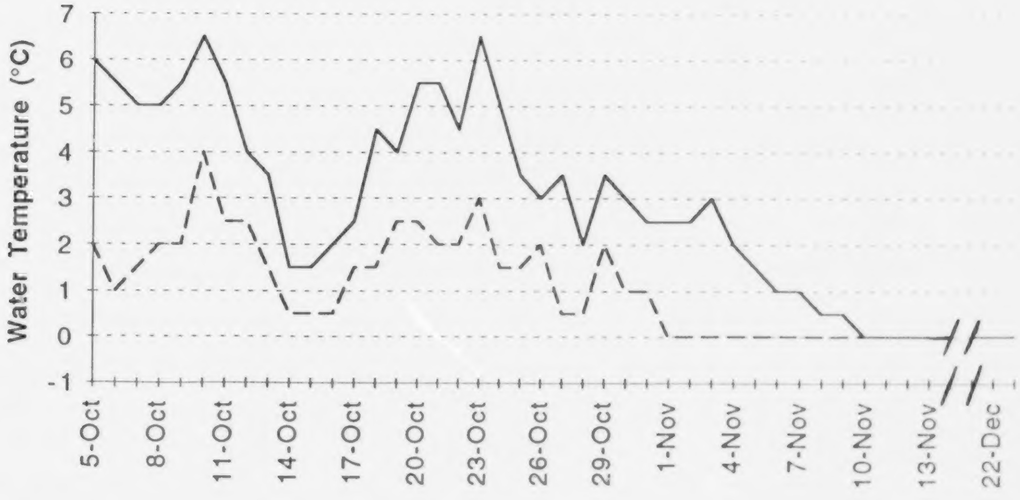


Figure 3-4. Maximum and minimum daily water temperatures (°C) in the Ram River drainage, fall-winter 1991 and 1992. Water temperatures were taken with Ryan thermographs which were placed in areas not influenced by groundwater input.

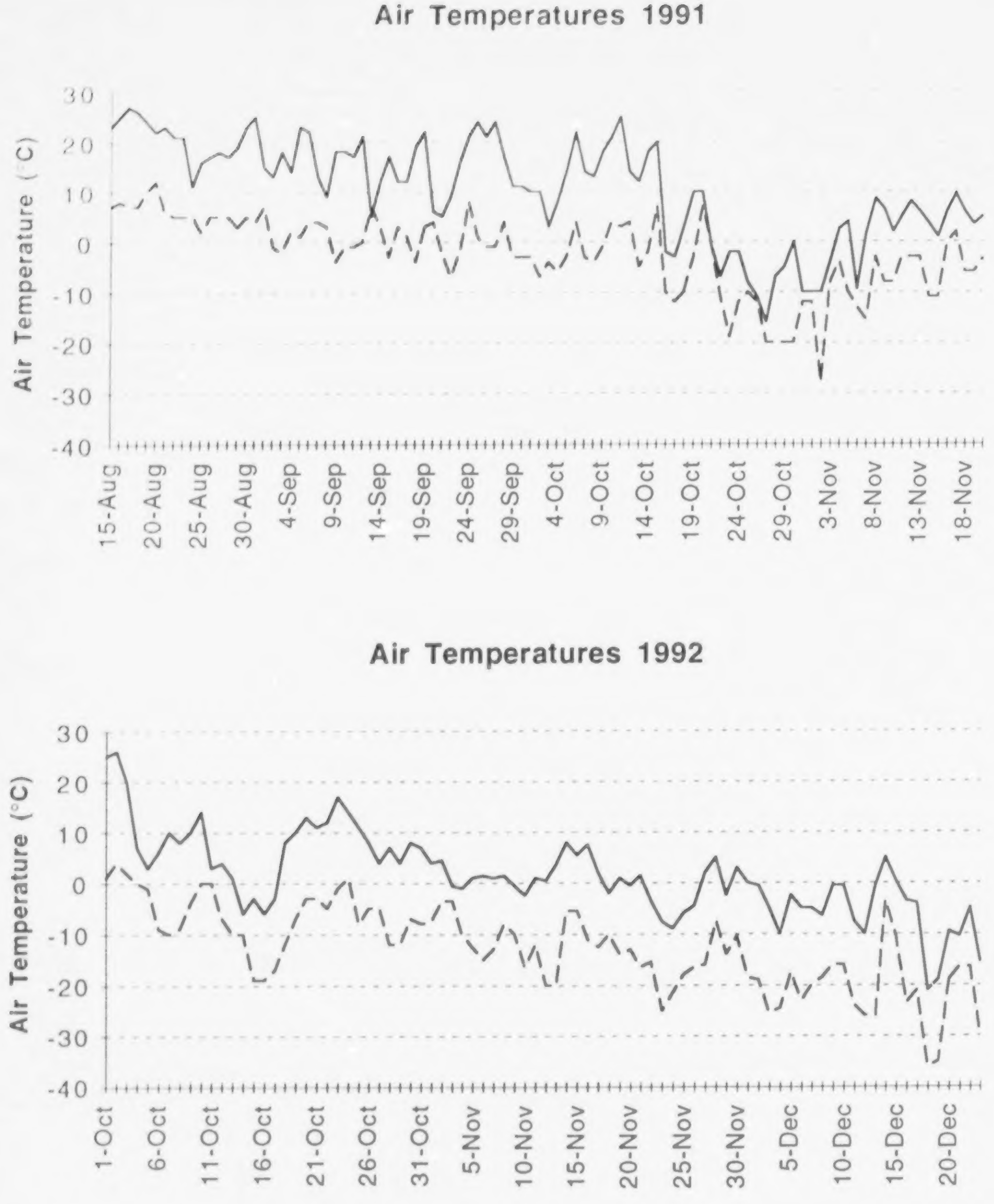


Figure 3-5. Maximum and minimum daily air temperatures (°C) in the Ram River area, fall-winter 1991 and 1992. The temperatures were obtained by averaging the daily maximum and minimum air temperatures from Environment Canada weather stations at Ram Falls (10 km east of the study area) and Nordegg (30 km North of the study area).

Table 3-5. Direction and distance moved, and date of arrival at overwintering areas for radiotagged cutthroat trout from the North Ram River, fall 1992.

Fish	Site	Moved to Overwintering Area			Last
#		Direction	Distance	Date	Location
23	NR 7	up	3.3	Dec. 7	Dec. 20
24	NR 7	up	0.6	Oct. 27	Dec. 20
25	NR 8	down	1.1	Nov. 19	Dec. 20
26	NR 9				Oct. 5[*]
27	NR 10	up	7.5	Nov. 19	Dec. 20
28	NR 12	down	1.2	Nov. 17	Dec. 20
29	NR 25				Oct. 28[+]
30	NR 25	down	3.0	Dec. 13	Dec. 20
31	NR 25	up	2.9	Nov. 13	Dec. 21
32	NR 25	up	0.4	Dec. 1	Dec. 20
33	NR 25				Oct. 5[*]
34	NR 25	up	0.3	Nov. 27	Dec. 20
35	NR 25				Oct. 11[+]
36	NR 25	up	2.9	Oct. 12	Dec. 21
37	NR 25	down	7.0	Dec. 7	Dec. 21
38	NR 25	up	2.9	Oct. 16	Dec. 21
39	NR 32	up	0.3	Nov. 13	Dec. 21
40	NR 32				Oct. 5[*]
41	NR 32				Oct. 10[#]
42	NR 32	up	7.6	Dec. 2	Dec. 5[†]
43	NR 32	up	0.3	Oct. 16	Dec. 21
44	NR 32	up	0.3	Oct. 22	Dec. 21
45	NR 32	none	0.0	by Oct. 31	Dec. 21

[+] Fish was found dead. [†] Fish moved out of study area. [*] Fish was lost. [#] Fish lost to predation.

Overwintering Areas

After the trout were forced out of staging pools, they moved to habitats where they could avoid frazil and anchor ice. Frazil and anchor ice does not form in areas where warm groundwater inflow keeps the stream temperatures above 0.0°C, or in areas covered by surface ice. Many of the overwintering areas were influenced by springs or groundwater discharging into the water column. By the end of December 1992, 13 radiotagged trout (77 %) were in areas influenced by warm water discharge. The remaining 4 (23 %) trout were in pools covered with surface ice. In these areas, the surface ice acted as an insulating blanket reducing radiant heat loss, so that the water did not become supercooled, and frazil ice did not form.

Some trout used more than one overwintering area. They moved to new overwintering areas as late as December 7. Only 4 fish out of 17 used more than one overwintering area. Of the 4 fish that used more than one overwintering area, 2 used 2 different areas and 2 used 3 different areas. Trout made movements of up to 3.2 km from one overwintering area to another.

Direction Trends

I found no significant difference ($P>0.05$) between the number of fish moving upstream and downstream to overwintering areas in 1991 or 1992. In 1991, 10 of 20 (50 %) trout moved upstream to overwintering areas, while 8 of 20 (40 %) moved downstream, and 2 of 20 (10 %) showed no movement during the time their locations were monitored (Table 3-4). In 1992, 12 of 17 (71 %) fish moved upstream to overwintering areas, 4 of 17 (24 %) moved downstream, and 1 of 17 (6 %) showed no movement during the time its locations were monitored (Table 3-5).

Although there was no trend in direction moved to overwintering areas, three of the five fish that used staging pools in 1991, staged in pools that were farther from their release point than their overwintering areas. These three fish moved 1.4-2.2 km to staging pools and then returned to areas within 600 m of their release point to overwinter. The other two fish moved to an overwintering pool that was 310 m upstream of their staging pool (1.4 km upstream of their release point).

Homing to Staging and Overwintering Areas

I also found that trout homed to the same overwintering locations in consecutive years. One female trout (fish #28; Table 3-2) was captured in a large pool on April 28, and implanted with a radio-transmitter. The trout was tracked through spawning and into its summer habitat by May 26. On October 15, the trout moved from the pool where it spent its summer (the same pool it was in May 26) to a staging pool. The trout was in the staging pool from October 22 to November 15. On November 17 it was found in the same pool where it had been captured and implanted April 28. The trout was still in this overwintering area when tracking ceased on December 20, 1992.

In both 1991 and 1992, I also observed trout aggregating in the same staging and overwintering pools. Two staging pools, and one overwintering pool used in 1991, Were also used in 1992. Radiotagged trout (2 in 1991; 3 in 1992) also moved from the same staging pool to the same overwintering pool. The fish were forced out of the staging pool by ice in both years.

Trout Moving Together

In addition to using the same staging and overwintering habitat yearly, trout showed other behavioural similarities. Some trout moved from different summer locations to the same staging area or overwintering area on the same day. Two trout from different locations moved upstream over 2 km to the same staging pool on Sept. 17, 1991. On Oct. 17, they had both moved downstream 1.9 km into the same overwintering pool.

Differences by Drainage

Although many trout moved to both staging and overwintering areas, not all trout exhibited the two step pattern of habitat use, the pattern varied slightly among drainages. By the end of October 1991, 30 % of the trout had aggregated in staging pools in the North Ram drainage, while only 20 % of the trout in the Onion drainage showed this behaviour. There was no significant difference (P>0.05) in the number of fish aggregating between drainages. Most of the trout that were implanted in 1992 (all in the North Ram Drainage) were captured after they had aggregated in staging pools and later they moved to overwintering pools.

While aggregating in both staging and overwintering areas was a common behaviour in the North Ram Drainage, it did not occur in the upper section of Onion Creek. In the upper reaches of Onion Creek there was a large amount of habitat where water temperatures were above 0.0° C throughout the winter. That is because Onion Creek, at its source, had a water temperature of 3.7°C. The water temperature slowly decreased to 0.0°C by the start of the fourth km below the source (at an air temperature of -8.7 to -9.5°C). Within this section of stream, the radiotagged trout (two) did not aggregate, and remained within a 100 m area from August to the end of October. Visual surveys were also done on December 10, 1992. During the survey, trout were observed to be distributed throughout the stream section and showed no indication of aggregation.

The first aggregation of fish noted in Onion Creek occurred downstream of the warm-water section. Aggregations were especially noted in areas where the stream was 0.0°C and seeps or tributaries entered. These small areas of warm groundwater inflow were 4-5°C warmer than the surrounding stream.

Even in areas with little warm water influx, a minority of fish did not aggregate. In the North Ram River (in 1991) at least 20 % of the fish were not in aggregations at their last location (Oct. 28-Nov. 17).

Movement Details

Whether the trout aggregated or not in the late fall and early winter, they exhibited a relatively stable pattern of movement. Most observations showed no movement in the 1-2 days between observations (84 % in 1991; 87 % in 1992), but when the trout did move, there were more long movements (>100 m; 64 % in 1991; 80 % in 1992) than short movements (<100 m; 36 % in 1991; 20 % in 1992).

The number of movements that trout made decreased from summer to winter (Figure 3-6). Fish had to move at least five meters from its previous location before it was considered to have moved. In 1991, the frequency of movement (# of movements / # observations) made by implanted fish was significantly ($P<0.05$) lower in September and October than August. The frequency of movement was also significantly ($P<0.05$) lower in October than September. This trend of decreasing frequency of movement with the onset of winter was significant ($P<0.05$) in both drainages. The mean number of moves individual fish made weekly during 1991 was 0.9 in August (Aug. 15-31), 0.6 in September, and 0.2 in October. While there was a significant decrease in number of movements from the summer to the fall of 1991, there was no

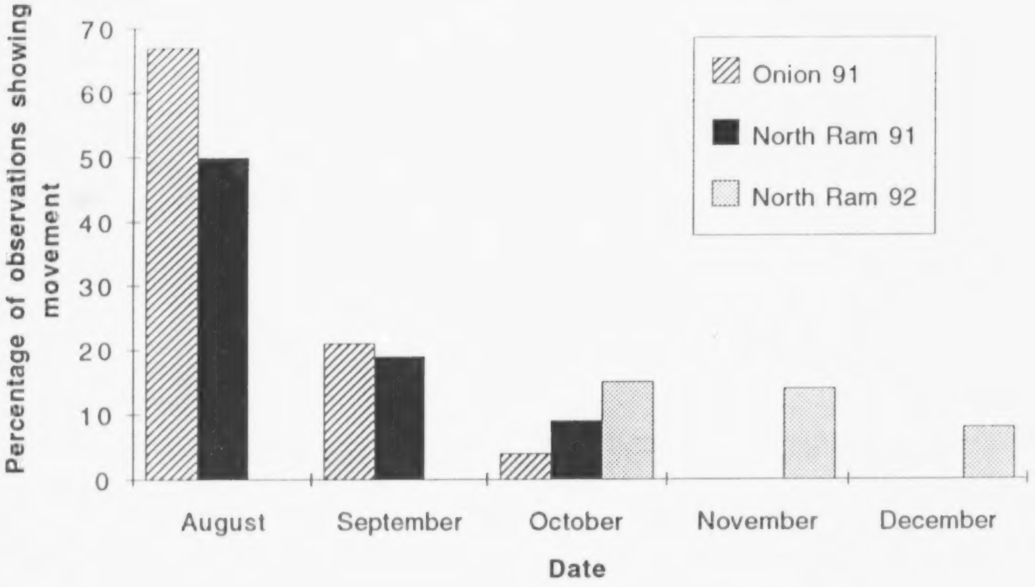


Figure 3-6. Percentage of observations of 45 cutthroat trout showing movement in the 2-3 days between trackings. Twenty-two cutthroat trout were tracked in the North Ram River and Onion Creek, Alberta from August to October, 1991 and 23 were tracked in the North Ram River, Alberta from October to December, 1992.

significant difference ($P<0.05$) in the frequency of movement from October to December, 1992.

Although there was no significant difference within 1992, there was a significantly ($P<0.05$) lower proportion of movements in October 1991 (North Ram and Onion drainages combined) than in October or November of 1992 (Fig. 3-6). Data for the two drainages in 1991 were grouped because there was no significant difference ($P>0.05$) in the frequency of movement between the drainages during August, September or October (Fig. 3-6). While there was a difference between the frequency of movements in October 1991 and October or November of 1992, there was no significant difference ($P<0.05$) between the proportion of trout moving in October 1991 and December, 1992 (Fig. 3-6). When the proportion of movements in North Ram River in October 1991 were compared to the North Ram in October 1992 there was no significant difference ($P>0.05$). However there was a significantly lower ($P<0.05$) proportion of movement in Onion Creek in October 1991 than in the North Ram River in October 1992.

Number of Fish and Observations

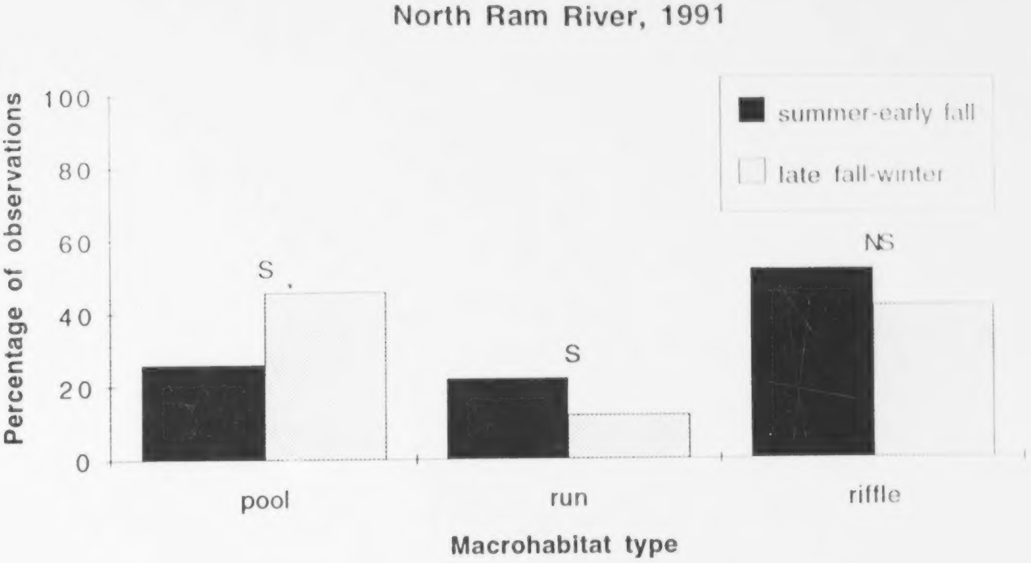
The movements and habitat use in fall and winter of 45 radiotagged cutthroat trout were examined throughout this study. Eighty-two percent of the radiotagged trout were successfully tracked to the end of the study period. Of the 22 cutthroat trout implanted with radio transmitters in 1991, one was not located after the first week of tracking and one was removed by an angler 12 days after implantation (Table 3-4). During the 62 days of tracking from Aug. 25 to Nov. 17, 1991, 510 observations were made. Of the 23 cutthroat trout implanted with radio transmitters in 1992, 5 were not located after the first week. Three of the five were lost, one was lost to predation, and the other was found dead. One other fish died within three weeks (Oct. 28) of implantation and was excluded from the study (Table 3-5). During the 45 tracking days from Oct. 8 - Dec. 21, 594 observations were made.

Macro-habitat Use

There were significant differences in macrohabitat use between drainages and between years. In 1991, total macrohabitat used (all dates combined) in Onion Creek was significantly ($P<0.05$) different from the North Ram River (Fig. 3-7). Macrohabitat use in both drainages during 1991 was significantly ($P<0.05$) different from macrohabitat use in the North Ram River during 1992 (Figure 3-8). Pools dominated macrohabitat use in Onion Creek during 1991, and the North Ram River during 1992, but not in the North Ram River the during summer-early fall, 1991.

In 1991, macrohabitat use change seasonally (Figures 3-7 and 3-8). The data were grouped as summer-early fall data (Aug. 15 - Sept. 15) and late fall-winter data (Sept. 16 - Dec. 30). Fish started moving to staging areas after Sept. 15. In the North Ram River, when fish moved to staging pools, the use of pools increased significantly ($P<0.05$) and the use of runs decreased significantly ($P<0.05$) (Figure 3-7). The use of riffles, however, did not change significantly ($P>0.05$). Although Onion Creek does not show the same pattern as the North Ram River, there was a change in macrohabitat use between late summer-early fall and late fall-winter in both drainages. Use of pools and riffles did not change significantly ($P>0.05$) but, similar to the North Ram River, the use of runs decreased significantly ($P<0.05$) (Figure 3-7).

In 1992, macrohabitat use changed from early October to late December in the North Ram River (Figure 3-8). The use of pools gradually decreased throughout the study period. Use of pools in December was significantly



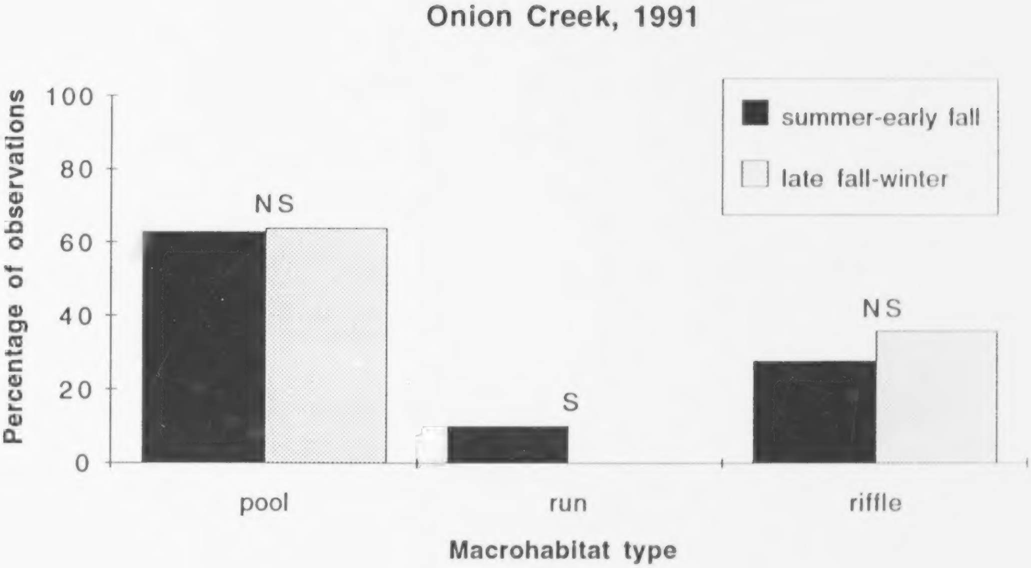


Figure 3-7. Percentage of observations of radiotagged cutthroat trout using three macrohabitat categories during summer-early fall (Aug. 15-Sept. 15) and late fall-winter (Sept. 16-Oct. 27), 1991. Significant (S; $P < 0.05$) and non-significant (NS) differences between seasons are indicated above each pair of bars.

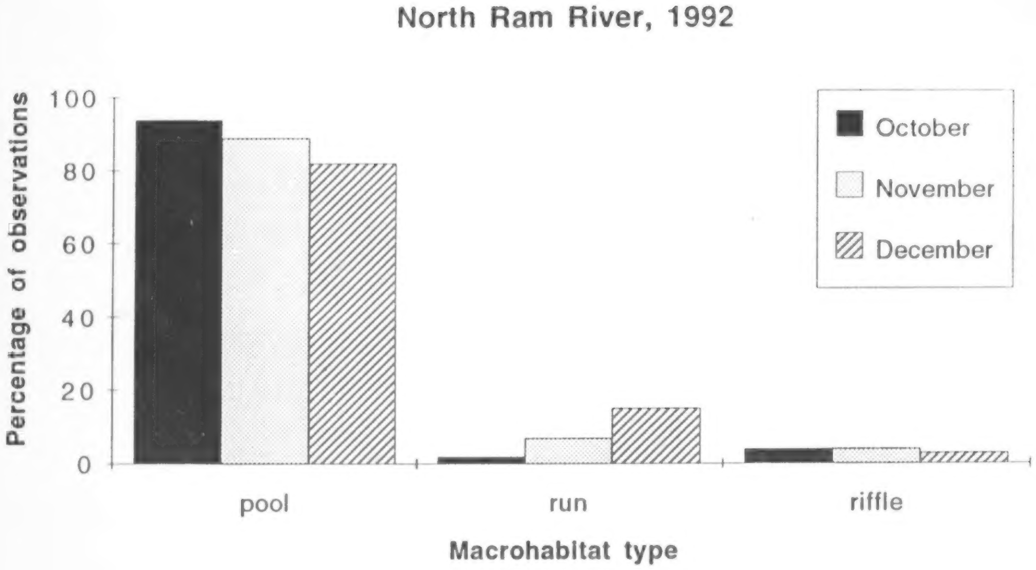


Figure 3-8. Percentage of observations of radiotagged cutthroat trout from the North Ram River, Alberta, using three macrohabitat categories, October-December, 1992.

($P<0.05$) lower than during October or November. While the use of riffles did not change significantly ($P>0.05$) the use of runs, opposite to the use of pools, gradually increased throughout the study period. The use of runs increased significantly ($P<0.05$) from October to November, and again from November to December (Fig. 3-8).

Macro-habitat Preferences

Macrohabitat use in most seasons and sites was significantly different ($P<0.05$) from macrohabitat available (Figures 3-9 and 3-10), illustrating preferences. Use of riffles was not significantly different ($P>0.05$) from availability of riffles in the North Ram River during either season. Use of macrohabitat was significantly different ($P<0.05$) from availability for all categories of macrohabitat in all other seasons and sites. All data for habitat use were not used for calculating preference values since habitat availability was not surveyed in all parts of the study area. Habitat use data were only used if the kilometer in which the data were obtained for use was surveyed for habitat availability. A mean of 84 % of the habitat use data were used to calculate preferences (84 % of the 1991 data from the North Ram River, 99 % of the 1991 data from Onion Creek, and 59 % of the 1992 data from the North Ram River). The 1991 data used for calculating preference values were not significantly different ($P<0.05$) from the total pool of habitat use data. The 1992 data used to calculate preferences, were, however, significantly different ($P<0.05$) from of the total pool of habitat use data.

When preference values were calculated, fish showed a preference for pools in all seasons and at all sites (Figures 3-11 and 3-12). When data for individuals were grouped, the preference of pools was significant ($P<0.05$) in all seasons and at all sites except in the North Ram River during the summer-early

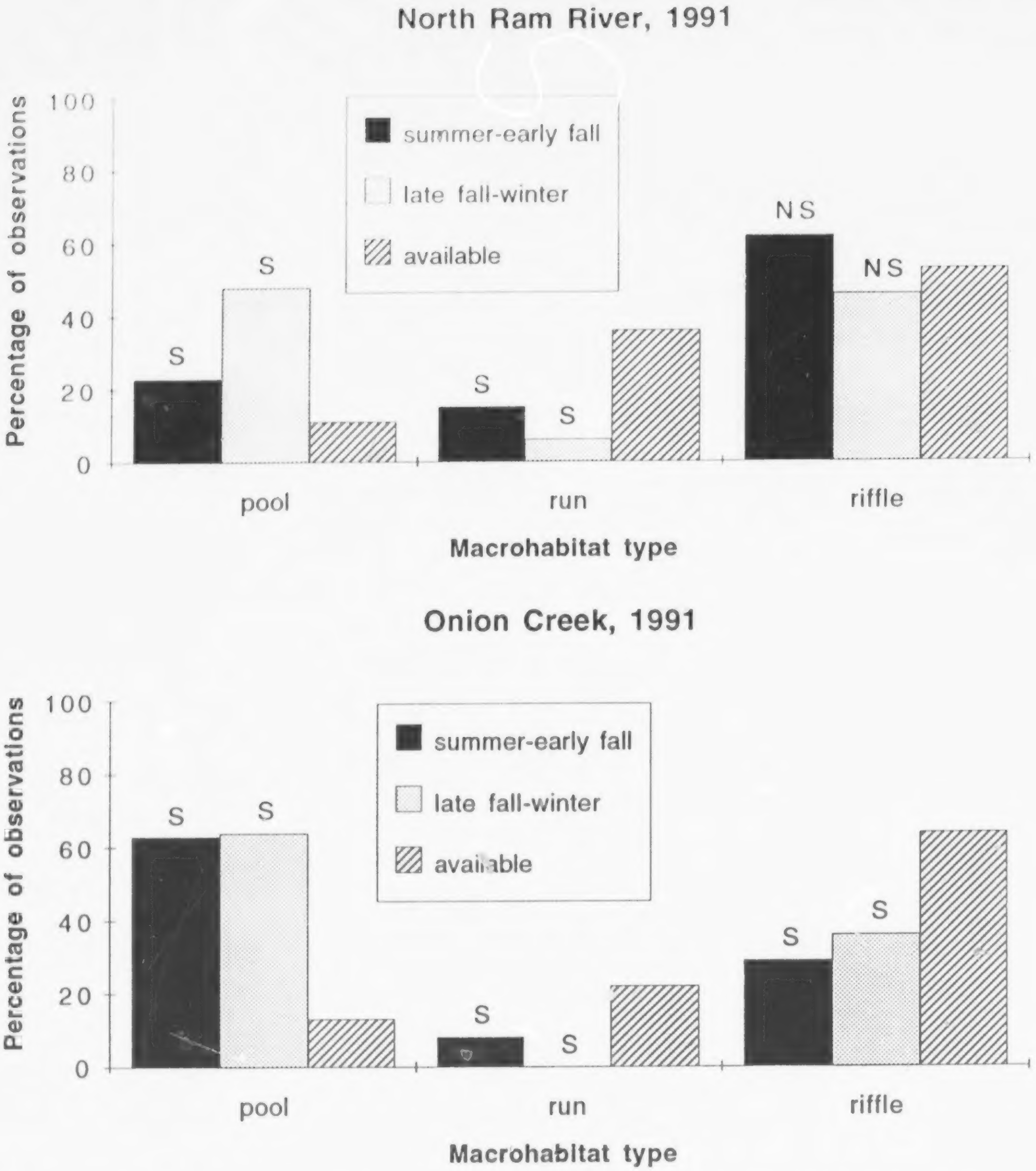


Figure 3-9. Percentage of observations of radiotagged cutthroat trout using three macrohabitat categories during summer-early fall (Aug. 15-Sept. 15) and late fall-winter (Sept. 16-Oct. 27), 1991. Percentage of each macrohabitat type recorded in habitat availability surveys is also shown. Data for habitat use is only from kilometers of the North Ram River or Onion Creek, Alberta, which were surveyed for habitat availability. Significant (S; $P < 0.05$) and non-significant (NS) differences between use and availability is indicated above each use bar.

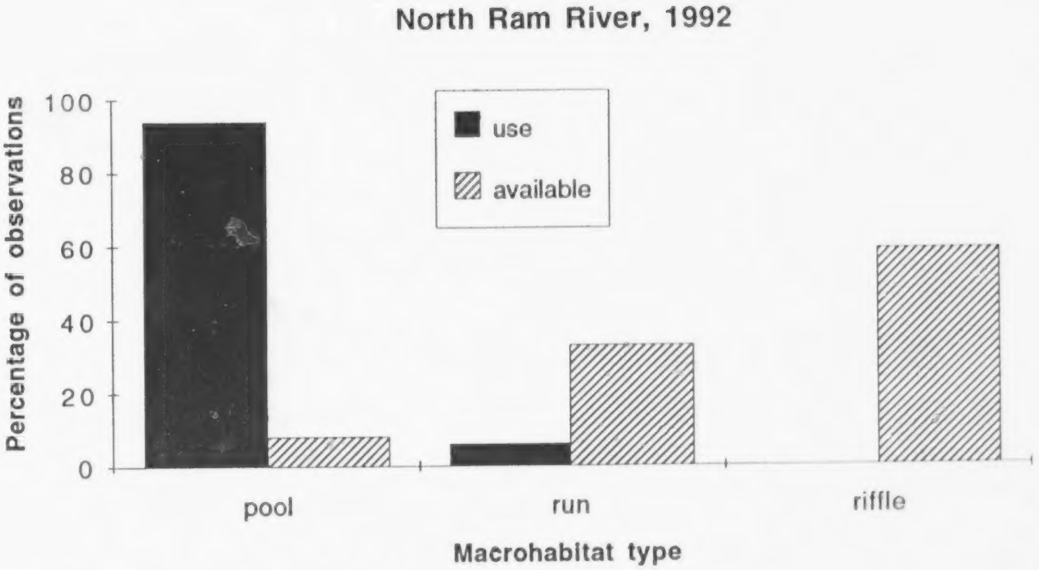
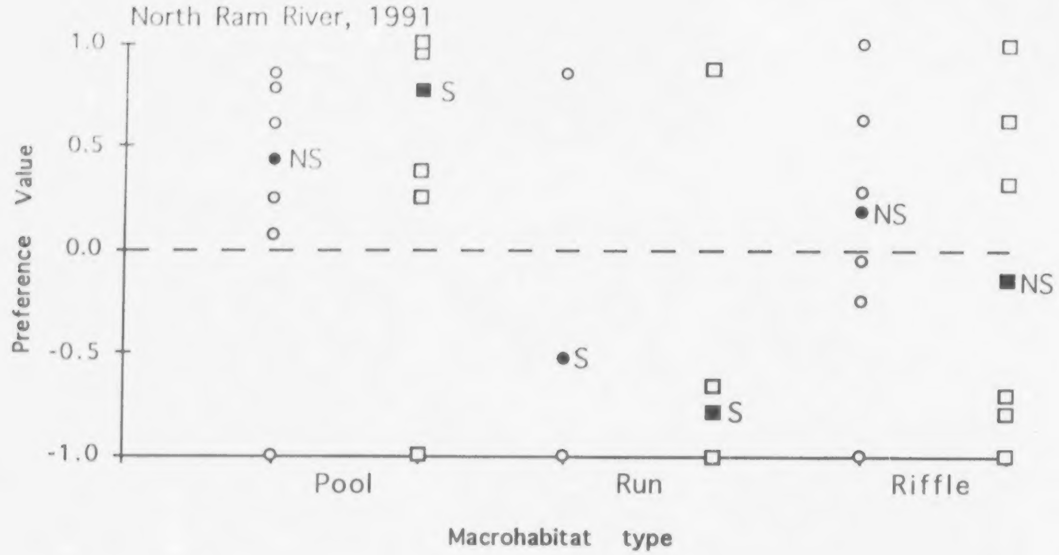


Figure 3-10. Percentage of observations of radiotagged cutthroat trout using three macrohabitat categories during, October-December, 1992. Percentage of each macrohabitat type recorded in habitat availability surveys is also shown. Data for habitat use is only from kilometers of the North Ram River, Alberta, which were surveyed for habitat availability. For each macrohabitat type, use is significantly ($P < 0.05$) different from availability.



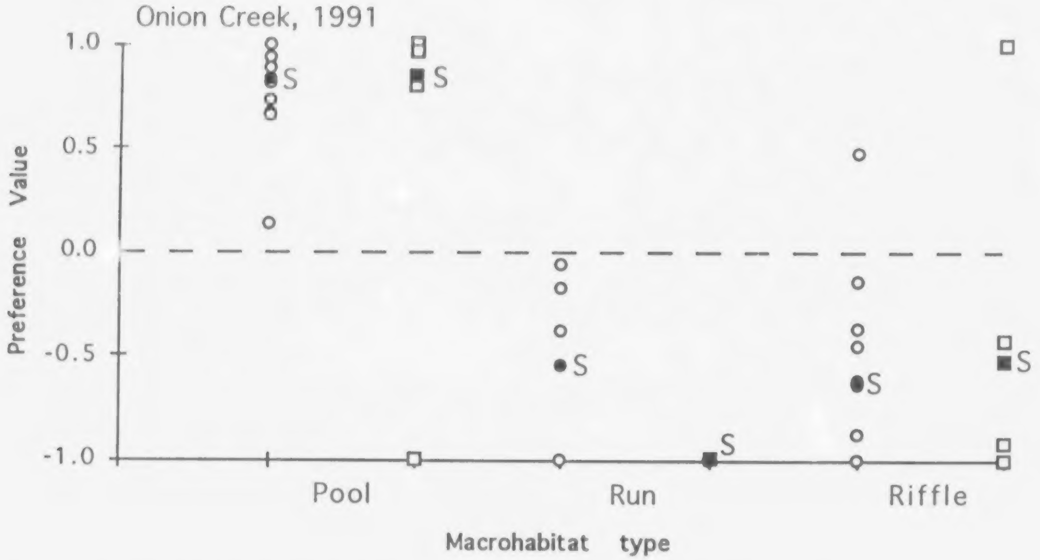


Figure 3-11. Individual (hollow symbols) and pooled (solid symbols) macrohabitat preference values for radiotagged cutthroat trout from the North Ram River and Onion Creek, Alberta, 1991. Data for summer-early fall (Aug. 15-Sept. 15) are shown as circles and data for late fall-winter (Sept. 16-Oct. 27) are shown as squares. Solid circles or squares are marked to indicate whether the preference value for grouped data is significant (S; $P < 0.05$) or not significant (NS).

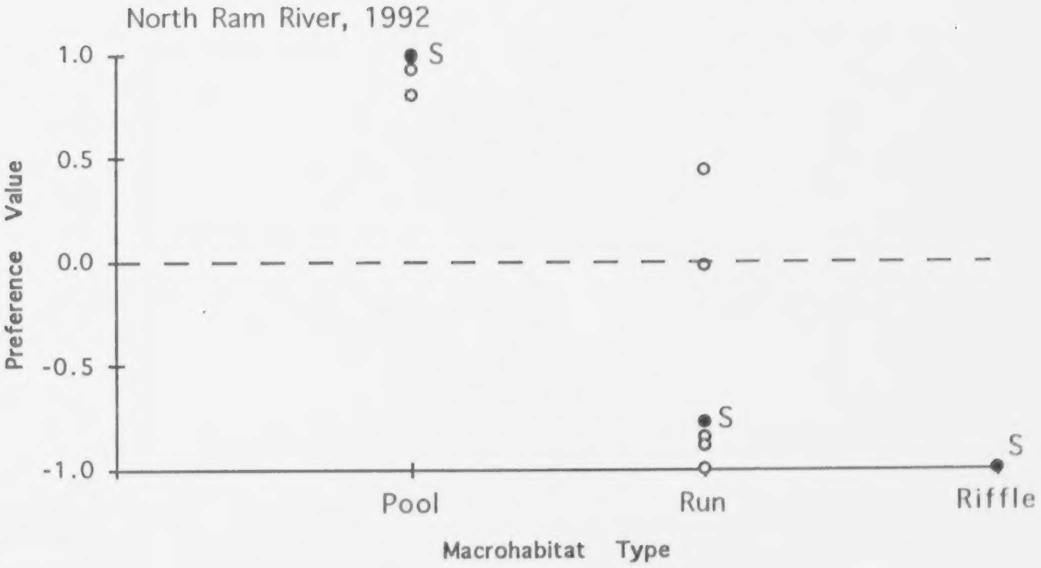


Figure 3-12. Individual (hollow circles) and pooled (solid circles) macrohabitat preference values for radiotagged cutthroat trout from the North Ram River, Alberta, October-December, 1992. Solid circles are marked to indicate whether the preference value for grouped data is significant (S; $P < 0.05$) or not significant (NS).

fall period (Figures 3-11 and 3-12). During the summer-early fall period, preference for pools was significantly higher ($P<0.05$) in Onion Creek than in the North Ram River. During the late fall-winter period, however, there was no significant ($P>0.05$) difference in preferences of pools between drainages.

Trout showed a strong avoidance (a preference value < -0.5) for runs in all seasons and sites. When data for individuals were grouped, the avoidance of runs was significant ($P<0.05$) in all seasons and sites (Figures 3-11 and 3-12). There was also no significant difference ($P>0.05$) in the preference values for runs between sites in either season.

Cutthroat trout avoided riffles in all seasons except during the late summer-early fall period in the North Ram River (Figures 3-11 and 3-12). When data for individuals were grouped, the avoidance of riffles was significant ($P<0.05$) in Onion Creek during both seasons and in the North Ram River during 1992. Fish in the North Ram River showed no significant preference for riffles in either season in 1991. During the summer-early fall period, preference values for riffles were significantly lower ($P<0.05$) in Onion Creek than in the North Ram River. During the late fall-early winter season, however, there was no significant difference ($P>0.05$) between sites in the preference values for riffles.

As winter approached, and trout shifted to staging habitat, macrohabitat use changed significantly ($P<0.05$) but macrohabitat preferences changed little. The only significant ($P<0.05$) seasonal change in macrohabitat was the decreased preference of runs in Onion Creek. During 1991, there was a general trend in both drainages of seasonal increases (insignificant, $P>0.05$) in the preference for pools (Figure 3-11), and decreases in the preference for runs.

Microhabitat Use

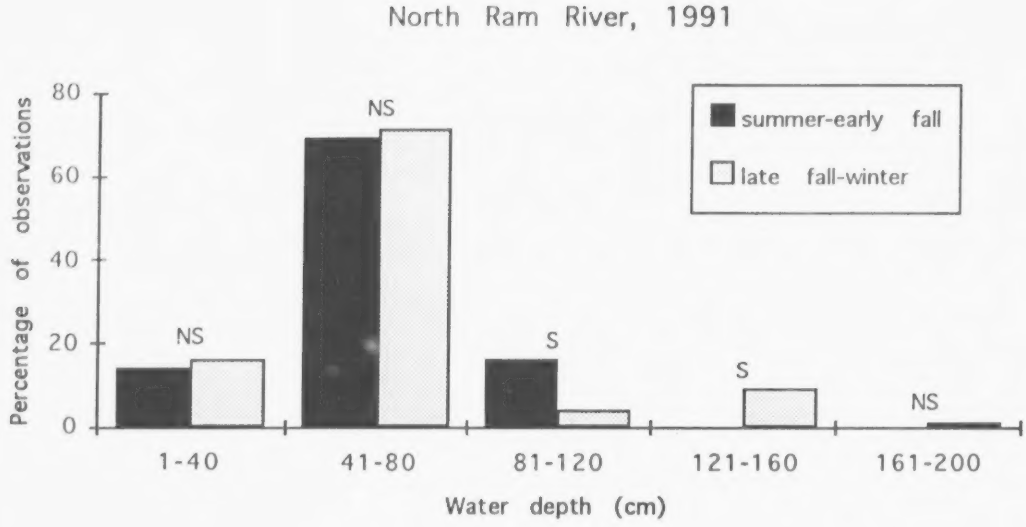
Depth

There were significant differences in water depth used between drainages and between years. In 1991, the water depths used in Onion Creek (median 49 cm, mean 61 cm) were significantly ($P<0.05$) lower than in the North Ram River (median 58 cm, mean 65 cm) (Fig. 3-13). The water depths used in both drainages from 1991 were significantly ($P<0.05$) lower than observations in the North Ram River (median 95 cm, mean 108 cm) during 1992 (Figure 3-13 and 3-14). Median depths are shown because data were not normally distributed so medians had to be compared using a Mann-Whitney U test.

Similar to macrohabitat use, water depth use also changed seasonally. During the first two weeks of September, the mean water depth used by trout was 61 cm (range 32-100 cm; $N=49$) in the North Ram drainage, and 69 cm (range 21-130 cm; $N=58$) in Onion Creek (Fig. 3-15). By the last half of October, 1991, trout in the North Ram drainage increased mean water depth used from 61 cm to 73 cm (range 30-148 cm;$N=39$). In the North Ram River, there was a gradual trend (insignificant, $P>0.05$) of increasing water depth use from early September to late October. In the Onion Creek, however, there was an opposite trend as water depth used decreased significantly ($P<0.05$) from the first two weeks in September (mean 69 cm) to the last half of October (mean 52 cm; Fig. 3-15; range 22-123 cm; $N=49$). Significant ($P<0.05$) seasonal changes in depth use were also found in both drainages when data were placed in categories of depth use (Fig. 3-13).

Depth Preferences

Water depth use in most seasons and sites was significantly different ($P<0.05$) from water depth available (Figures 3-16 and 3-17), illustrating



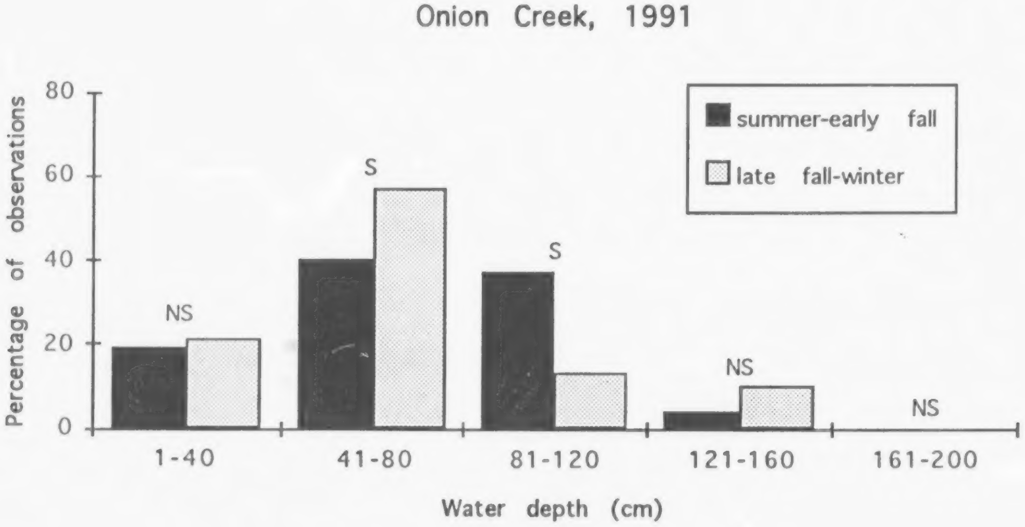


Figure 3-13. Percentage of observations of radiotagged cutthroat trout using five water depth categories during summer-early fall (Aug. 15-Sept. 15) and late fall-winter (Sept. 16-Oct. 27), 1991. Significant (S; $P < 0.05$) or non-significant (NS) changes between seasons are indicated above each pair of bars.

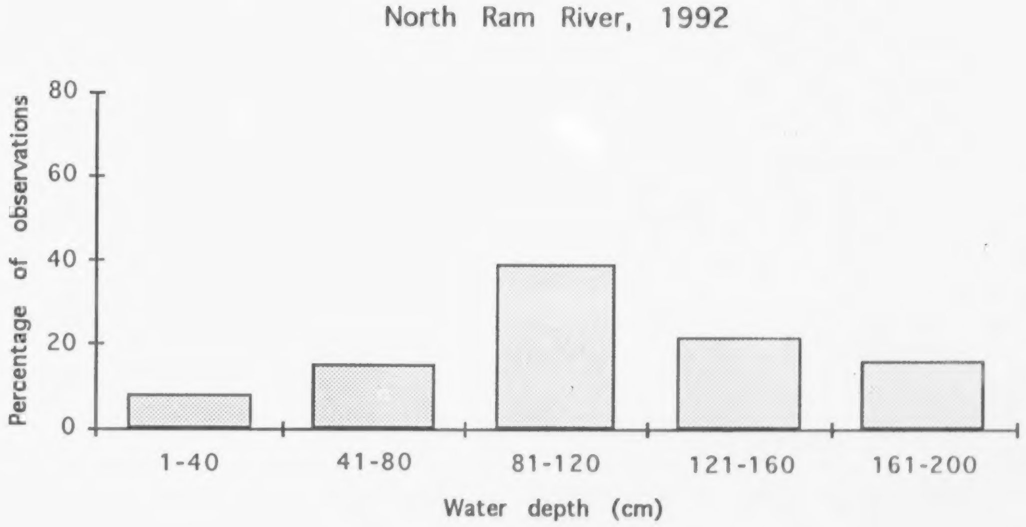


Figure 3-14. Percentage of observations of radiotagged cutthroat trout from the North Ram River, Alberta, using five water depth categories, October-December, 1992.

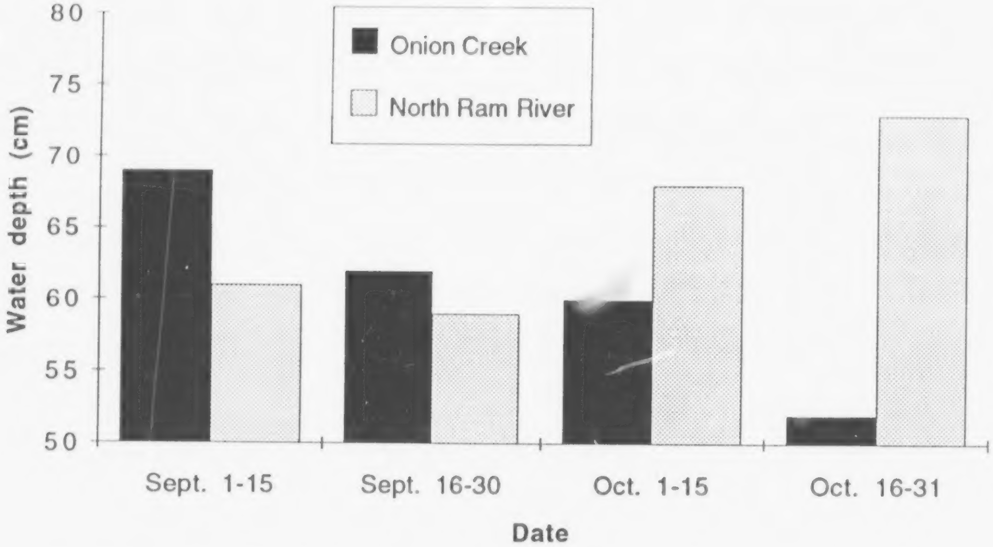
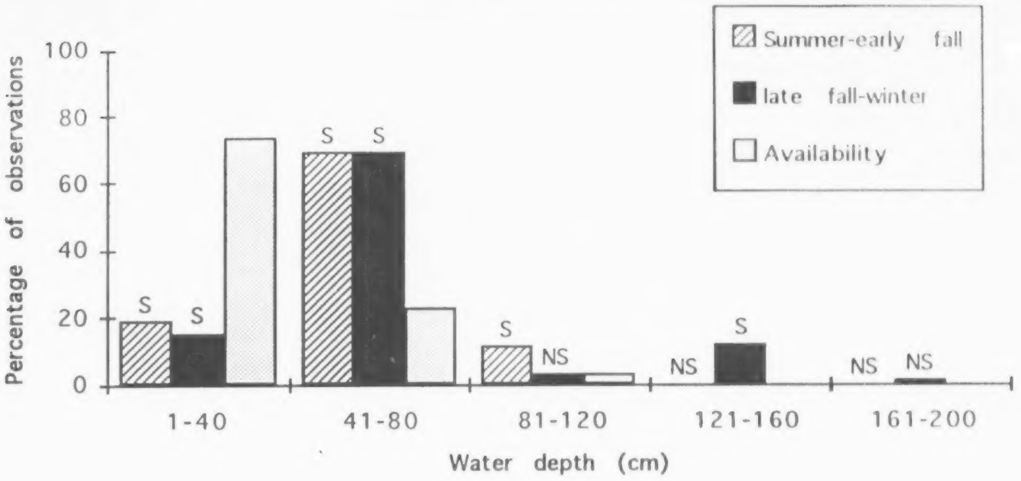


Figure 3-15. Mean water depths used by radiotagged cutthroat trout from the North Ram River and Onion Creek, Alberta, during September and October, 1991.

North Ram River, 1991



Onion Creek, 1991

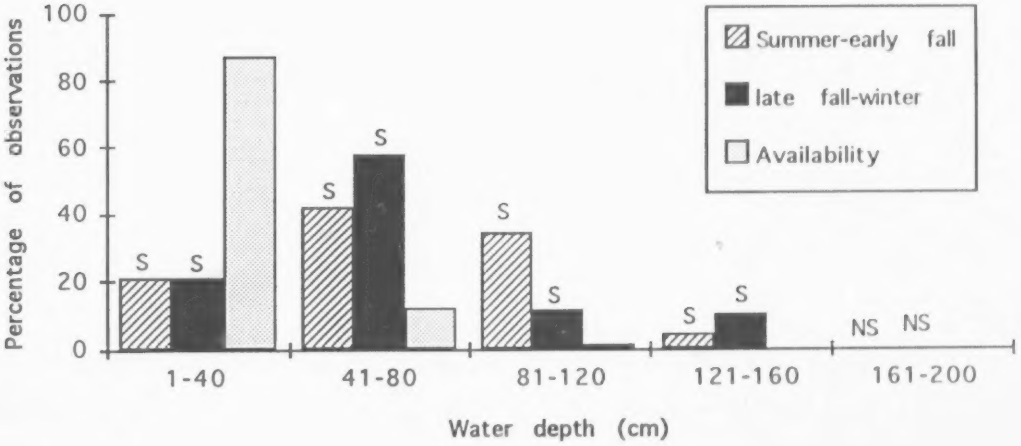


Figure 3-16. Percentage of observations of radiotagged cutthroat trout using five water depth categories during summer-early fall (Aug. 15-Sept. 15) and late fall-winter (Sept. 16-Oct. 27), 1991. Percentage of each water depth category recorded in habitat availability surveys is also shown. Data for water depth use is only from kilometers of the North Ram River or Onion Creek, Alberta, which were surveyed for water depth availability. Significant (S; $P < 0.05$) or non-significant (NS) differences between use and availability are indicated above each use bar.

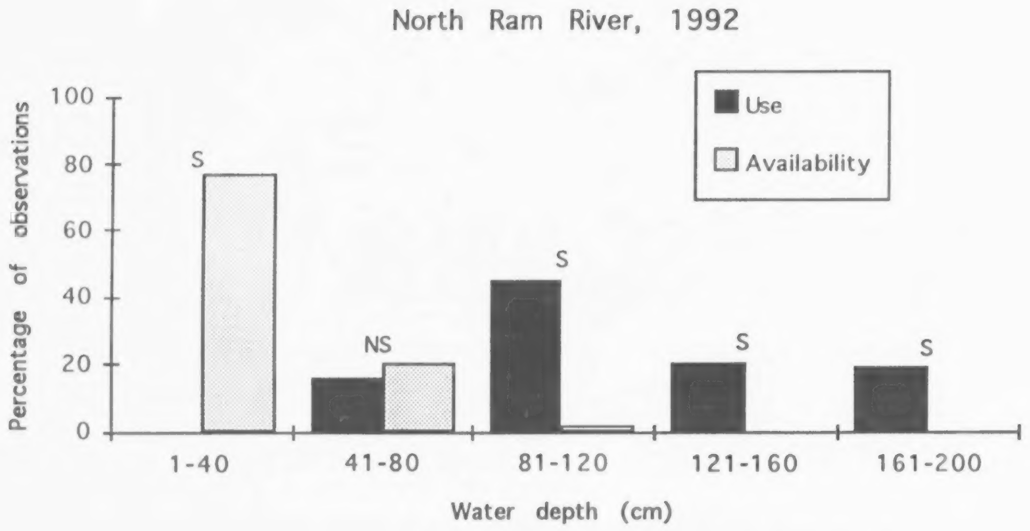
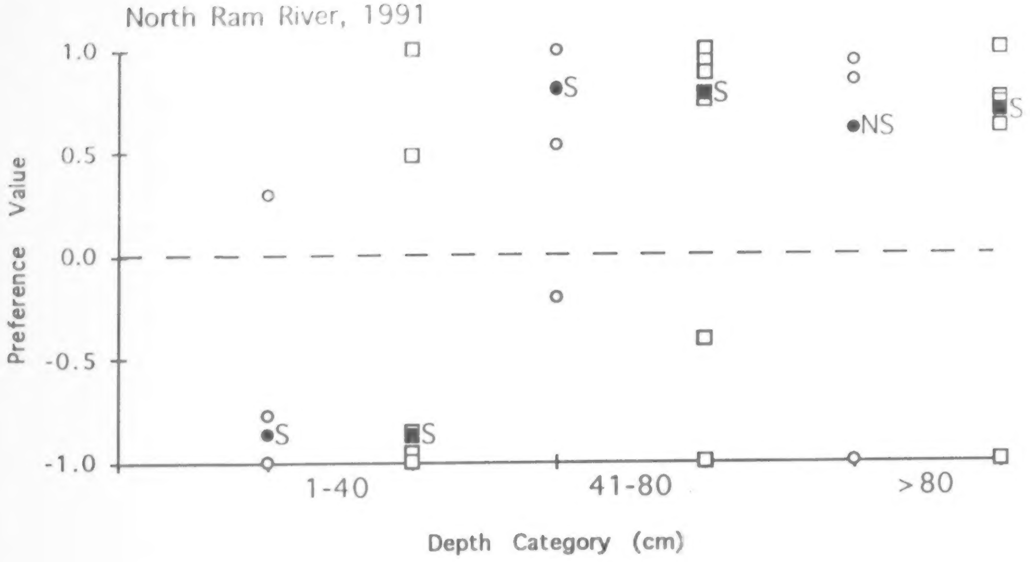


Figure 3-17. Percentage of observations of radiotagged cutthroat trout using five water depth categories, October-December, 1992. Percentage of each water depth category recorded in habitat availability surveys is also shown. Data for water depth use is only from kilometers of the North Ram River, Alberta, which were surveyed for water depth availability. Significant (S; $P < 0.05$) or non-significant (NS) differences between use and availability are indicated above each use bar.

preferences (Figures 3-18 and 3-19). Similar to macrohabitat use, all the data available for water depth use were not employed for calculating preference values since water depth availability was not surveyed in all parts of the study area. Water depth use data (Figures 3-16 and 3-17) were only used if the kilometer in which the data were obtained was surveyed for habitat availability. A mean of 78 % of the water depth use data were used to calculate preferences (90 % of the 1991 data from the North Ram River, 100 % of the 1991 data from Onion Creek, and 61 % of the 1992 data from the North Ram River). The 1991 data used for calculating preference values were not significantly different ($P<0.05$) from the total 1991 pool of depth use data for all kilometers. The 1992 data used to calculate preferences, were however, significantly different ($P<0.05$) from of the total pool of 1992 depth use data. If the lowest water depth category (0-40 cm) was deleted, the 1992 data used to calculate preferences, were not significantly different ($P>0.05$) from of the total pool of water depth use data

Water depths over 80 cm were preferred in all seasons and drainages in both 1991 and 1992, while shallower (from 0-40 cm) depths were avoided in all seasons and at all sites (Figures 3-18 and 3-19). During 1991, there was also a strong preference for depths over 40 cm in both seasons, while there was no significant ($P>0.05$) preference for the 40-80 cm depth class in 1992. During 1991, there were no significant differences ($P>0.05$) in preference values for depth between sites or between seasons. There was also no significant ($P>0.05$) correlation between water depth and preference values in either site or in either season of 1991. In 1992, however, there was a significant ($P<0.05$) positive correlation between preference values and water depth.



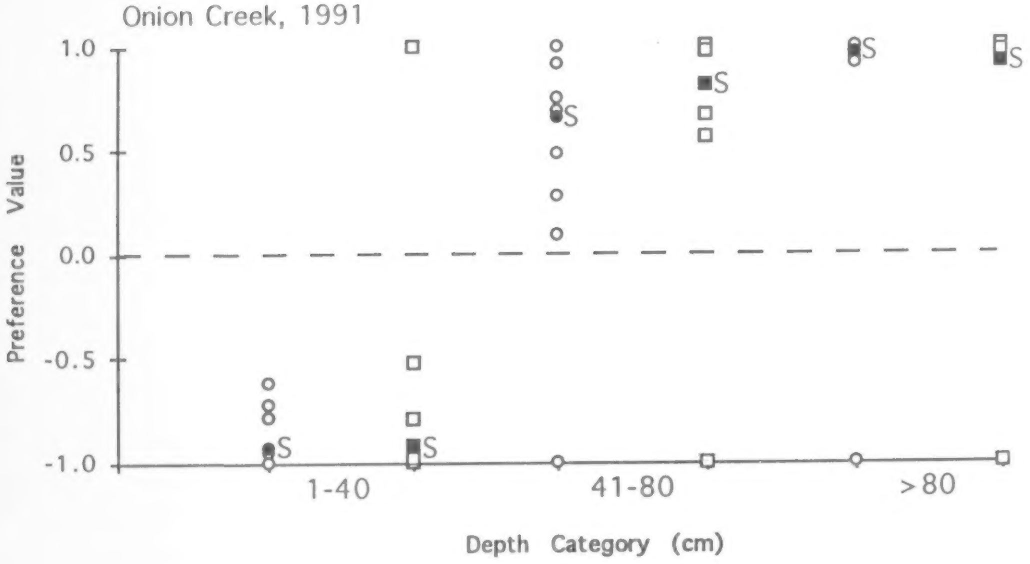


Figure 3-18. Individual (hollow symbols) and pooled (solid symbols) water depth preference values for radiotagged cutthroat trout from the North Ram River and Onion Creek, Alberta, 1991. Data for summer-early fall (Aug. 15-Sept. 15) are shown as circles and data for late fall-winter (Sept. 16-Oct. 27) are shown as squares. Solid circles or squares are marked to indicate whether the preference value for grouped data is significant (S; P < 0.05) or not significant (NS).

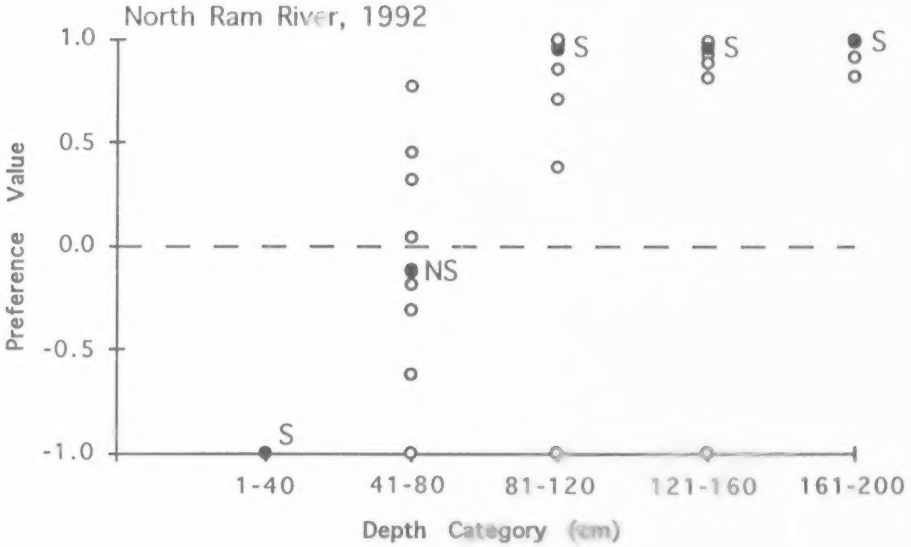


Figure 3-19. Individual (hollow circles) and pooled (solid circles) water depth preference values for radiotagged cutthroat trout from the North Ram River, Alberta, October-December, 1992. Solid circles are marked to indicate whether the preference value for grouped data is significant (S; $P < 0.05$) or not significant (NS).

Cover

Use of cover also changed seasonally. Fish in the North Ram River used cover significantly ($P<0.05$) less during the late fall-winter period (84-85 %) than from the late summer-fall period (98 %). In Onion Creek, however, trout were within 0.5 m of cover at 100 % of the observations during the entire study period.

Many overwintering pools used in the North Ram River did not have cover present. At the end of the study period in 1992, none of the overwintering areas that were affected by warm water influx contained cover. Thus, 77 % of trout were not within 0.5 m of cover in overwintering habitat in the North Ram River during 1992.

The type of cover used varied between sites. The dominant type of cover used in Onion Creek was undercut banks, while in the North Ram River, large woody debris (mostly fallen trees and logs) was the most commonly used cover type. Cover preference was not calculated since cover was recorded in less than two percent of the observations of habitat available.

Substrate Use

There were significant differences in substrate use between drainages and between years. In 1991, total substrate used (all dates combined) in Onion Creek was significantly ($P<0.05$) different from that used in the North Ram River (Figure 3-20). Substrate use in both drainages from 1991 was significantly ($P<0.05$) different from observations in the North Ram River during 1992 (Figure 3-21). Substrate use was not dominated by any one category in any of the sites or years.

In 1991, substrate use changed from the summer-early fall season to the late fall-winter season (Figure 3-20). The trends of the seasonal changes in

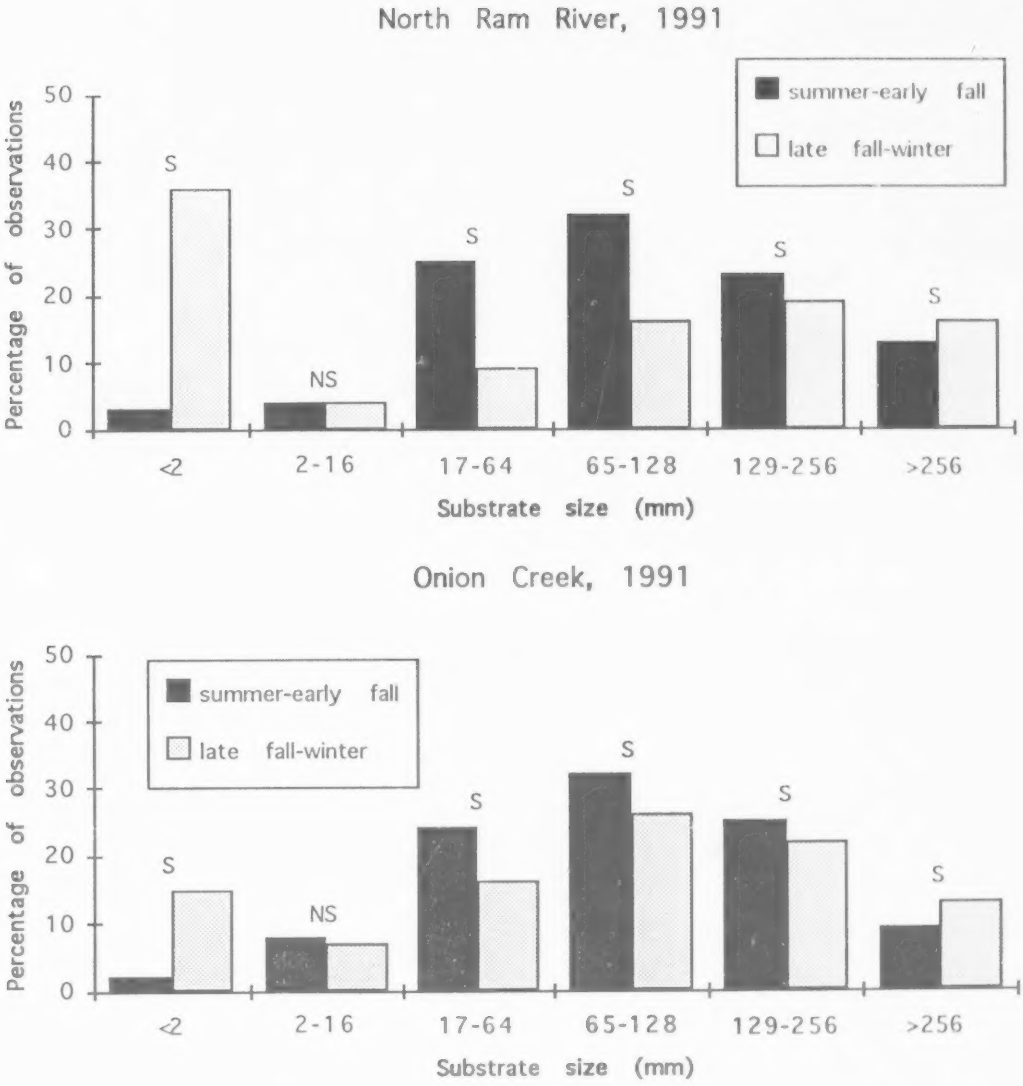


Figure 3-20. Percentage of observations of radiotagged cutthroat trout using six substrate categories during summer-early fall (Aug. 15-Sept. 15) and late fall-winter (Sept. 16-Oct. 27), 1991. Significant (S; $P < 0.05$) or non-significant (NS) changes between seasons are indicated above each pair of bars.

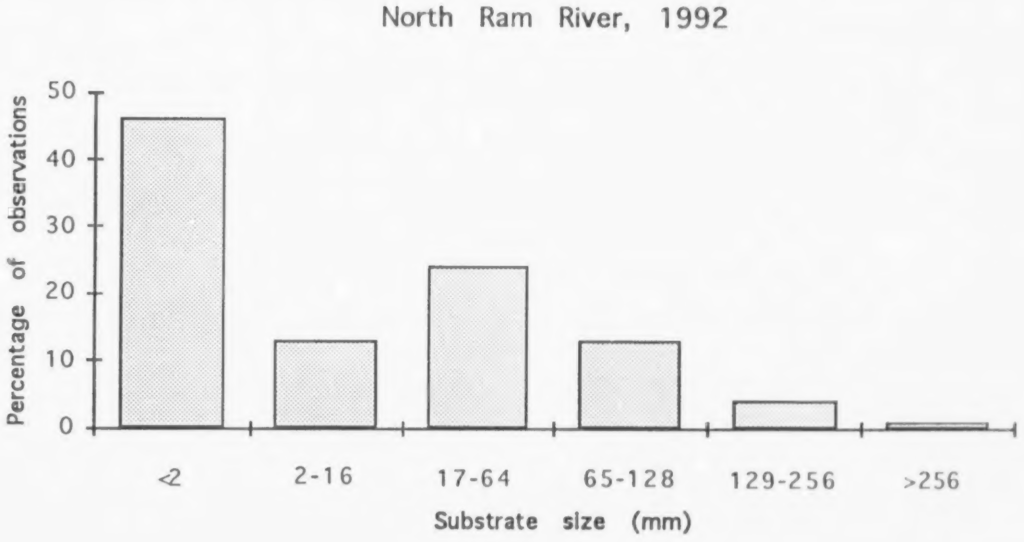


Figure 3-21. Percentage of observations of radiotagged cutthroat trout from the North Ram River, Alberta, using six substrate categories, October-December, 1992.

substrate use were very similar in both drainages. In both the North Ram River and Onion Creek, when fish moved to staging pools (after September 15) the use of fines (<2 mm) and boulders (>256 mm) increased significantly ($P<0.05$) and the use of large gravel, small and large cobble (17-256 mm) decreased significantly ($P<0.05$). In both Onion Creek and the North Ram River, small gravel (2-16 mm) was the only category which did not have a significant ($P<0.05$) seasonal change in use.

Substrate use in most seasons and sites was significantly different ($P<0.05$) from substrate available (Figures 3-22 and 3-23), illustrating preferences (Figures 3-24 - 3-26). Similar to macrohabitat and depth use, not all data for substrate use were employed for calculating preference values since substrate availability was not surveyed in all parts of the study area. A mean of 75 % of the substrate use data were used to calculate preferences (90 % of the 1991 data from the North Ram River, 100 % of the 1991 data from Onion Creek, and 59 % of the 1992 data from the North Ram River). The North Ram River data (for both years) used to calculate preferences were significantly different ($P<0.05$) from of the substrate habitat use data.

Substrate Preferences

In the summer-early fall season of 1991, there were few similarities in substrate preferences between the two drainages (Figures 3-24 and 3-25). This is reflected in the significant ($P<0.05$) differences in preferences between the two drainages in half of the substrate categories (2-16 mm, 17-64 mm, and 129-256 mm). In the summer-early fall season of 1991, there was a significant ($P<0.05$) positive correlation between substrate preferences and increasing sizes of substrate in Onion Creek, but there was no significant ($P>0.05$)

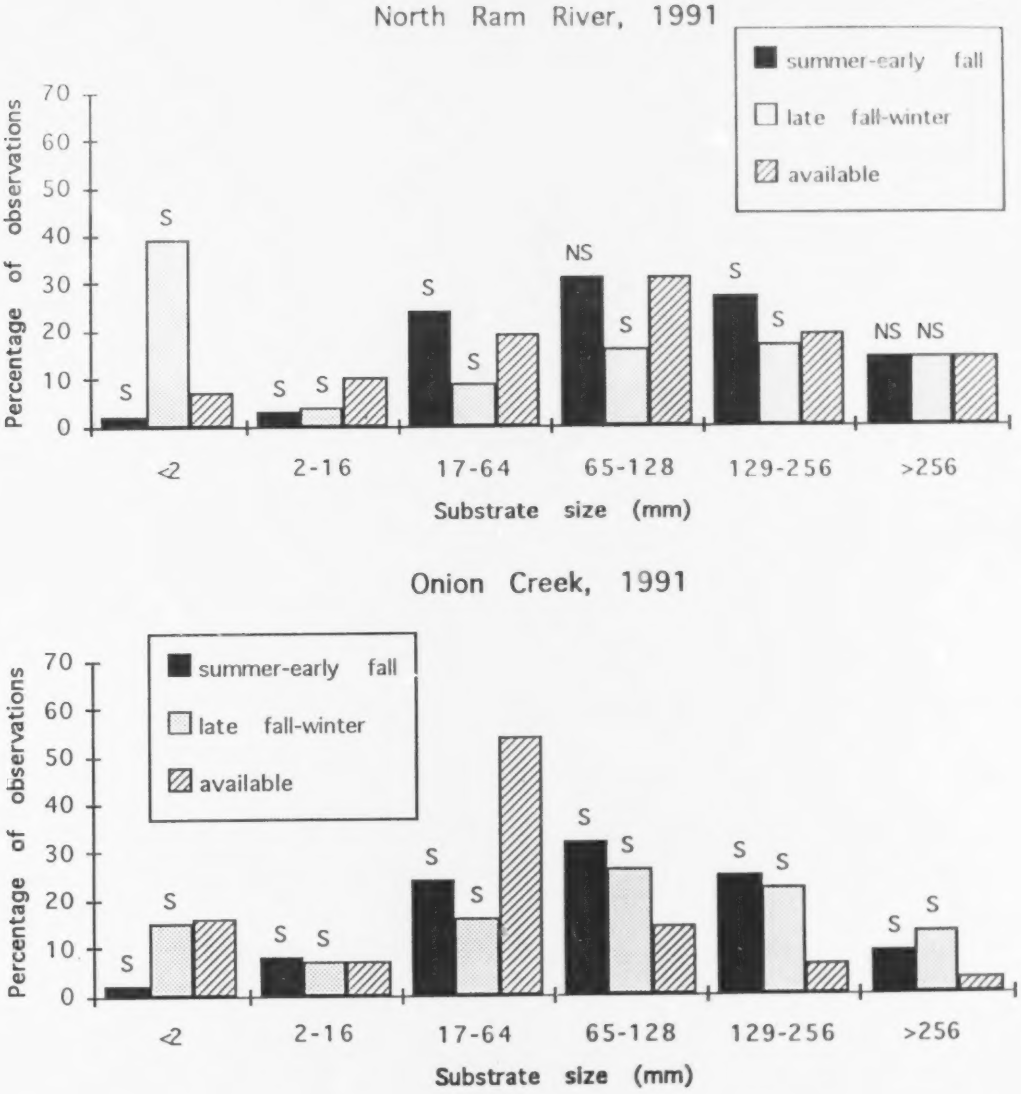


Figure 3-22. Percentage of observations of radiotagged cutthroat trout using six substrate categories during summer-early fall (Aug. 15-Sept. 15) and late fall-winter (Sept. 16-Oct. 27), 1991. Percentage of each substrate category recorded in habitat availability surveys is also shown. Data for substrate use is only from kilometers of the North Ram River or Onion Creek, Alberta, which were surveyed for substrate availability. Significant (S; $P < 0.05$) or non-significant (NS) differences between use and availability are indicated above each use bar.

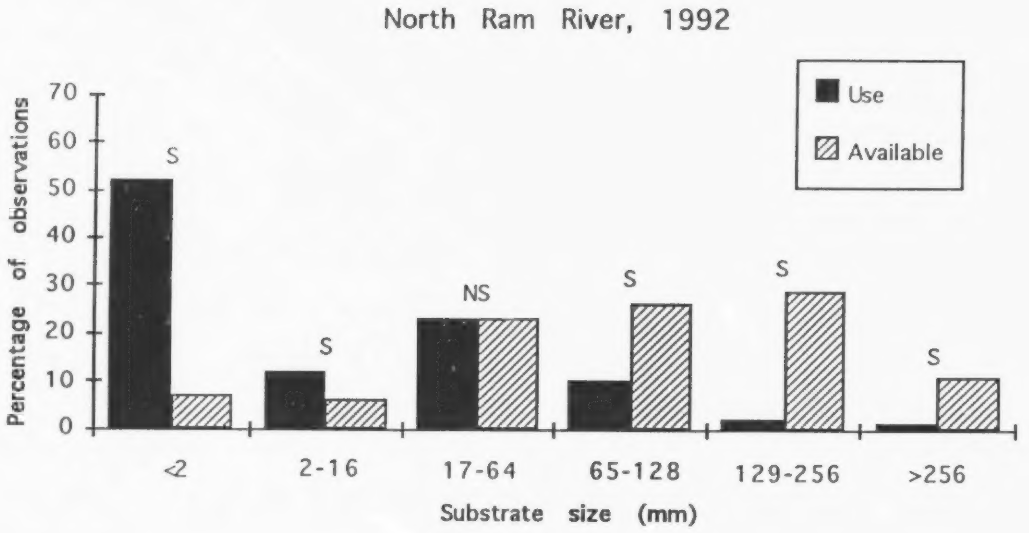


Figure 3-23. Percentage of observations of radiotagged cutthroat trout using six substrate categories, October-December, 1992. Percentage of each substrate category recorded in habitat availability surveys is also shown. Data for substrate use is only from kilometers of the North Ram River or Onion Creek, Alberta, which were surveyed for substrate availability. Significant (S; $P < 0.05$) or non-significant (NS) differences between use and availability are indicated above each use bar.

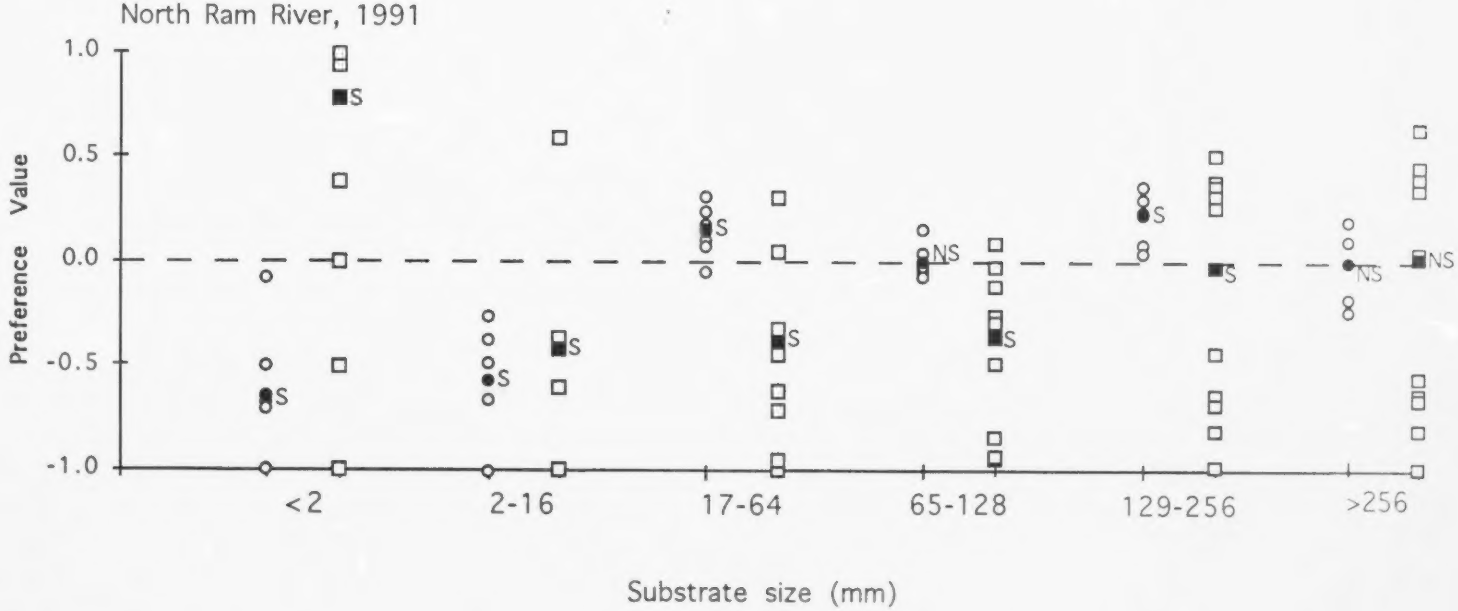


Figure 3-24. Individual (hollow circles) and pooled (solid circles) substrate preference values for radiotagged cutthroat trout from the North Ram River, Alberta, 1991. Data for summer-early fall (Aug. 15-Sept. 15) are shown as circles and data for late fall-winter (Sept. 16-Oct. 27) are shown as squares. Solid circles or squares are marked to indicate whether the preference value for grouped data is significant (S; $\underline{P} < 0.05$) or not significant (NS).

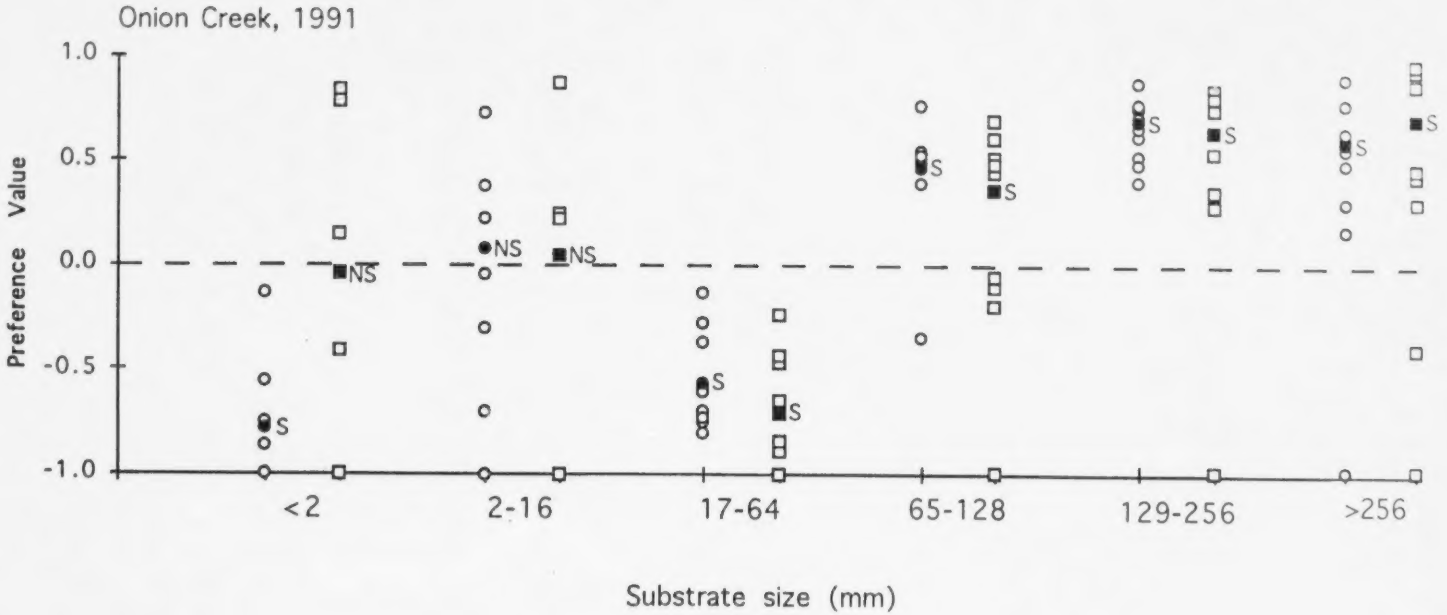


Figure 3-25. Individual (hollow circles) and pooled (solid circles) substrate preference values for radiotagged cutthroat trout from Onion Creek, Alberta, 1991. Data for summer-early fall (Aug. 15-Sept. 15) are shown as circles and data for late fall-winter (Sept. 16-Oct. 27) are shown as squares. Solid circles or squares are marked to indicate whether the preference value for grouped data is significant (S; $\underline{P} < 0.05$) or not significant (NS).

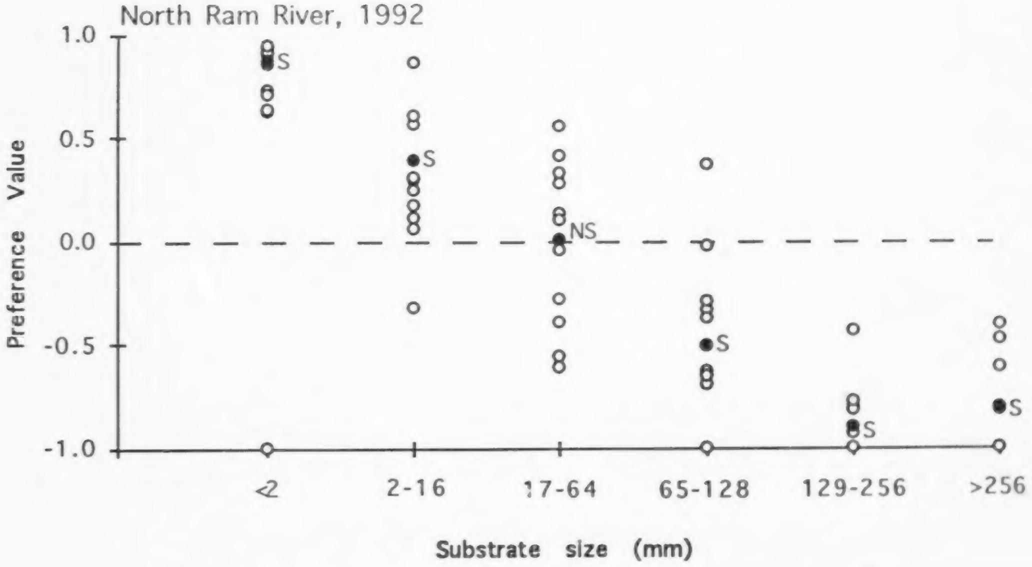


Figure 3-26. Individual (hollow circles) and pooled (solid circles) substrate preference values for radiotagged cutthroat trout from the North Ram River, Alberta, October-December, 1992. Solid circles are marked to indicate whether the preference value for grouped data is significant (S; P < 0.05) or not significant (NS).

correlation between substrate preferences and sizes of substrate In the North Ram River.

In the late fall-winter season, there were no significant ($P>0.05$) differences in the substrate preferences between the two sites. There were also no significant ($P>0.05$) correlations between substrate preferences and sizes of substrate.

There were few significant ($P<0.05$) seasonal changes in substrate use. In Onion Creek (Figure 3-25), the only large (yet insignificant , $P>0.05$) change was the increased preference for fine substrates (<2 mm). In the North Ram River, two of the larger substrate categories (17-128 mm) showed significant ($P<0.05$) decreases in preference. This reflects a general pattern of seasonal decreased use of the larger sized substrates.

During 1992, finer substrates were used, and preferred more than the rougher substrates (Figure 3-26). The preference of substrates decreased as the roughness of the substrate increased, fines (<2 mm) being the most preferred and large cobble and boulders the least preferred. There was a significant ($P<0.05$) negative correlation between preference values and substrate size.

Discussion

Two Stage Habitat Shift

The behaviour associated with the first shift in habitat use can be attributed to the change in physiological needs trout have with the onset of winter. In the summer, trout exhibit territorial behaviour to maximize feeding and growth. As water temperatures decrease, so does the metabolism of the trout. At some threshold, trout may shift from a strategy of feeding and growth, to a strategy of conserving energy and finding protection from the perils of winter (Cunjak and Power 1986).

I found decreasing water temperatures were associated with trout moving out of summer habitat by the last half of September. The habitat that trout shifted to is similar to that described for overwintering by others, as areas of low water velocity (Cunjak and Power 1986, Chisholm *et al.* 1987, Meyers *et al.* 1992), dense cover (Cunjak and Power 1986, Heggenes 1991b), and relatively deep water (Hartman 1965, Chisholm *et al.* 1987). In this habitat, trout aggregated in large numbers, similar to behaviour noted by Cunjak and Power (1986) and Hartman (1965). They found brook and brown trout aggregating both in the summer and winter, but aggregation sizes increased with declining water temperatures. A breakdown in territoriality at colder temperatures has also been noted by others such as Baltz *et al.* (1991) who found trout less segregated in the fall than summer. A decrease in aggression in winter was also noted by Hartman (1965).

Due to the harsh winter conditions in the Ram system, I found a second stage to the overwintering movement behaviour. Since the trout aggregated in pools and later moved to other areas to overwinter, I called these pools 'staging' pools. When the habitat in staging pools was eliminated by formation of anchor ice on the cover, trout moved to other areas which were not influenced by frazil and anchor ice. While the water is supercooled, frazil ice is more likely to be adhesive (Carstens 1966) and sticks to objects under the water surface, forming anchor ice (Osterkamp and Gosink 1982; Tsang 1982). The logs and branches that were abundant in the staging pools became blanketed with anchor ice. As frazil and anchor ice moves with the current, it can adhere to other anchor ice formations. Frazil ice can also attach to anchor ice by the interlocking of ice crystals (Tsang 1982). By either direct adhesion or the interlocking of ice particles, anchor ice grew to such an extent that it completely filled the staging pools where trout aggregated early in the fall. The trout probably would have stayed in their initial habitat if they hadn't been excluded by frazil and anchor ice. Anchor ice has been observed by other fisheries researchers (Needham and Slater 1944, Maciolek and Needham 1952, Needham and Jones 1959), but direct shifts in habitat use related to anchor ice formation have not been documented. Studies of winter habitat use in milder areas, like that done by Heggenes *et al.* (1991b) fail to find this second habitat shift because milder weather precludes frazil and anchor ice formation.

Distance to Overwintering Areas

The results of this study did not support the hypothesis that cutthroat trout would move long distances downstream to find overwintering habitat. While the movements I found are not as extensive as Bjornn and Mallet (1964) reported, most are not as limited as suggested by Miller (1954, 1957), or found by Heggenes *et al.* (1991a) in a milder coastal climate. The radiotagged trout likely didn't move as much as those Bjornn and Mallet (1964) studied since adequate overwintering habitat was available within a few kilometers of summer habitat. Most, however, moved more than trout studied in coastal British Columbia streams because harsher weather excluded large portions of habitat from use.

The 1.0-2.4 km mean overwintering movements I found are very similar to the limited (less than 500 m) overwintering movements of radiotagged brook trout observed by Chisholm *et al.* (1987). Similar to habitat in the Ram River drainage, the habitat in Chisholm's *et al.* (1987) study area was not poor enough to drive trout from the streams, nor was the climate mild enough to allow trout to stay in a small home range throughout the year.

The amount of preferred winter habitat available can determine the extent of fall movements (Hunt 1974). If preferred habitat is not available to trout, they will migrate to find it (Hunt 1974), but when researchers experimentally increased overwintering habitat (the amount of pool area, and overhanging streambank cover) fewer brook trout moved downstream in the fall (Hunt 1974). If overwintering habitat was experimentally increased or decreased in the Ram River system I would expect the trout, in turn, to make shorter or longer movements to find suitable overwintering habitat. The important point that can be derived from this is that trout readily adapt to their environment, making adequate movements to fulfill their needs.

Staging Pools

Staging pools are similar to overwintering areas in milder climates, having low water velocities, relatively deep water, and abundant cover. Other researchers have found trout using this type of habitat during fall and winter (Cunjak and Power 1986, Chisholm *et al.* 1987).

Cover may be a very important consideration for fall habitat. Most of the staging pools contained woody debris consisting of log jams, beaver caches, or a combination of the two. Cover was found to be an important winter habitat parameter by Cunjak and Power (1986), Heggenes *et al.* (1991b), and Hartman (1965). Since four of the five staging pools contained beaver caches, the beavers provided a valuable source of cover. Impounded areas behind beaver dams are also important overwintering habitat in other areas (Chisholm *et al.* 1987).

The cover in the staging pools may be very important for predator avoidance. Although trout in the Ram drainage have no piscivorous fish species as predators, mergansers are important predators in the fall. Raptors and birds that migrate in the fall (like mergansers) could constitute a major source of predation on trout. Mink may have a large impact in both the fall and winter. One radiotransmitter was found chewed up by a mink, laying on the bank at the side of a staging pool. There was no indication that the trout was in poor health. The large aggregations, as this trout was in, may make predation easier, although less likely for each individual.

Since 60 % of the fish initially moved past overwintering areas to staging areas, I suspect that the staging areas are preferred by the trout but are unavailable later in the winter due to ice exclusion. If the overwintering areas were preferred, the trout would likely not have moved past them to staging pools, but would have stayed in these areas initially. That is unless the habitat available in the overwintering areas was different at that time, which it probably was not. The staging pools could be more preferred because the cover may decrease the chance of predation by birds and mink.

Frazil and Anchor Ice

Frazil and anchor ice had a great effect on availability of trout habitat in the winter. The appearance of these ice forms excluded most of the habitat used in the fall. This forced fish to use areas which were often devoid of cover. Our observations of trout using little cover in the winter are contradictory to the findings of other researchers who found trout using cover more in winter than summer (Cunjak and Power 1986). Using less cover could increase the amount of predation.

The presence of frazil ice may have caused direct mortality. Ten trout were found in the North Ram River, laying dead on the bottom of the river. I suspect that they were either directly suffocated by frazil ice, as Tack (1938) found, or were engulfed and crushed when the river was filled with anchor ice.

Levels of frazil and anchor ice varied among stream stretches, because of warm water influx. The amount of warm water input is likely a key factor in the date trout shifted from staging to overwintering habitat. Where no groundwater input occurred, trout likely move to overwintering areas earlier, but in areas with a small amount of warm water, they may not move to overwintering areas until very cold air temperatures occur, this is suggested by our findings. In areas with just a small amount of groundwater influx, the area may commonly be subject to frazil and anchor ice. Some of these small sources were used as overwintering areas for aggregations of trout. In these areas, survival is very fragile and just enough warm water may be available to keep the fish from being overcome by ice, even slight external influences by human activity could cause death.

In some parts of the drainage, frazil ice occurs throughout the winter. In these areas, groundwater influx keeps surface ice from forming and there is a transition zone between ice covered and ice free areas. Frazil and anchor ice occurred often in these transition zones. This situation may be common during winter below dams in high gradient rivers. In these areas, the water released from dams is above 0.0°C and, if hydraulics are favourable, may produce massive amounts of frazil ice as it cools.

In lower elevation areas I found little anchor ice because the river was mostly covered with surface ice, however, it did occur in riffles where flow was fast enough to prevent surface ice formation. Frazil ice can form in these open riffles and get washed down into surface ice covered pools and glides. In ice covered river sections, frazil ice can adhere to the bottom of the surface ice and thick layers of ice build downward into the pool, this is called a hanging dam (Tsang 1982). As hanging dams grow downward, the area of flowing water between the ice and the stream bottom decreases. As the depth of flowing water decreases, the water velocity in the pool increases. The buildup of frazil ice on the hanging dam can continue to increase until the water velocity reaches a critical velocity, where frazil ice cannot stick to the hanging dam because the flow is too fast (Tsang 1982). The ice covered pools, where large aggregations of trout take refuge for the winter, may be filled with hanging dams and hydraulic conditions can undergo drastic changes, forcing fish to move to new habitat. The fish may also be forced to search for new habitat while the water column is filled with frazil ice. The effects this phenomenon has on fish should be examined since it could be a major cause of winter mortality. Mortalities of this type could be totally overlooked since dead fish would be under surface ice.

Overwintering Areas

The factors that made overwintering areas distinct is that they didn't have frazil or anchor ice present. Since frazil ice adheres to woody debris, a majority (77 %) of the trout (in 1992) overwintered in pools or glides where no cover was present. This is much different than the large degree of cover use found by others (Cunjak and Power 1986, Heggenes 1991b).

Some (23 % in 1992) of the trout overwintered in pools covered with surface ice. All of these fish were in the low elevation section of the North Ram River where surface ice cover was dominant. This is similar to the habitat that brook trout used in Wyoming streams (Chisholm *et al.* 1987), where trout overwintered in areas impounded by beaver dams and in stream sections covered with snow. In areas with surface ice or snow cover, trout are protected from supercooled water temperatures and avian predators.

Warm water influx played a very important role in winter habitat selection. I found a majority (77 % in 1992) of trout using areas influenced by groundwater, this is also supported by Cunjak and Power's (1986) findings. They found 18 of 19 aggregations in water 2.0-6.0°C warmer than the main stream.

Warm water is probably a more important factor in winter habitat choice than depth. This is supported by our observations of one trout which overwintered in water as shallow as 8 cm. Cunjak and Power (1986) also suggested that water depth is probably most important where it provides protection from water current or provides cover with depth.

Directional Trends

While moving to overwintering areas, cutthroat trout did not illustrate a directional trend. Our findings are unlike those of most researchers who found trout moving downstream to overwinter (Bjornn and Mallet 1964, Chapman and Bjornn 1969, Bjornn 1971, Peterson 1982, Chisholm *et al.* 1987). Conversely, I observed several fish moving upstream to overwintering areas as far as 7.6 km. Chisholm *et al.* (1987) noted that most of the radiotagged brook trout they studied made net downstream movements, only one of the fifteen trout moved upstream to overwinter.

Homing To Staging and Overwintering Areas

Trout can home to the same overwintering areas in consecutive years. While it is common for trout to home to spawning areas, there is no documentation of homing to overwintering areas. One trout was tracked from its overwintering area through spawning, to its summer habitat, a staging pool, and again back to the same overwintering pool on Nov. 17, 1992.

The homing of this trout to the same overwintering area illustrates the importance of overwintering habitat. This trout spent 7 months in spawning, summer, and staging habitat. It is likely that in the remaining five months of the year (late Nov. - late April), this trout resides in only one pool. Since such a large portion of the trout's life is spent in overwintering habitat, a better effort to understand the needs of trout during winter is essential.

I also observed that the same staging and overwintering areas were used in both 1991 and 1992, and 3 implanted trout moved from the same staging pool to the same overwintering pool in 1992, as 2 other implanted trout did in 1991. This confirms that the two stage overwintering movements were not just an isolated case happening only in one year. It also reemphasizes the importance of both staging and overwintering areas to trout. If an abundance of these habitats were available, trout may have used a wider variety of locations.

Trout Moving Together

While some fish appear to move into staging and overwintering areas together, others move to the same area but on different days. The fish appear to move from all directions into the areas with the best habitat. Cunjak and Power (1986), describe this as a "clumping" or "squeezing" effect, which can occur when fish have limited spatial commodities.

Trout moving long distances (over 2 km) to staging or overwintering areas on the same dates may suggest trout are moving together, following each other, or environmental factors may stimulate trout to move at the same time. Since environmental stimulus to make movements is common during spawning, causing large numbers of trout to move simultaneously, it is not unreasonable to think a similar type of response to environmental conditions could cause trout to move to other types of habitat in the fall. Cooling temperatures and ice formation likely cause shifts to overwintering habitat in the same way that increasing temperatures and rising water flows cause the initiation of spawning movements. Photoperiod could also play a role in movements to overwintering areas just as it does in timing of spawning (Morrison and Smith 1986).

Differences by Drainage

Aggregation in staging and overwintering areas was more prevalent in the North Ram River than in Onion Creek. This is probably because overwintering habitat appeared to be more limited in the North Ram River than in Onion Creek. Large stretches of warm water habitat made aggregation unnecessary in parts of Onion Creek. In these warm water areas, neither radiotagged or visually observed trout were found aggregating. Cunjak and Power (1986) describe how fish are squeezed into suitable winter habitat as a result of little suitable habitat available. This is one of the mechanisms behind aggregation, the spatial limitation of habitat (Cunjak and Power 1986). In the upper section of Onion Creek, warm water was distributed over several kilometers of stream, along with abundant cover. Since suitable habitat was abundant, trout were not forced to aggregate. In the Ram River system, aggregations occurred only in areas where warm water showed a patchy distribution or was absent. The trout aggregated in areas where small amounts of groundwater were present but were not seen aggregating where long stretches of groundwater influenced habitat were present, and cover and water depth were adequate.

In much of Onion Creek, the stream was sheltered from harsh overwintering conditions by surface ice and snow bridges. The surface ice and snow bridges insulated much of the creek from supercooling, precluding frazil and anchor ice formation. Snow bridging was also observed in high altitude Wyoming streams by Chisholm *et al.* (1987). The abundance of protected habitat may also have reduced the need to aggregate.

There may also be two different strategies in overwintering survival. Some of the fish may stay in isolated areas throughout the winter, while the rest reside in aggregations. This difference is found between brook and brown trout overwintering behaviour. Cunjak and Power (1986) found most brook trout exhibited gregarious behaviour but brown trout exhibited a more solitary winter distribution. In the Ram system, there may be different overwintering strategies in areas not influenced by long stretches of warm water, or it could be that I did not track trout long enough in 1991 to observe all of them move into overwintering areas and aggregate. Since many of the trout did not move to overwintering areas until November, during 1992, it is likely that all fish did not make the second habitat transition during 1991 until after intensive monitoring ended on Oct. 28. Also, since all of the fish that were tracked in 1992 were always observed with other fish, I suggest that most of the fish I implanted in 1991 would overwinter in aggregations unless they overwintered in large stretches which were influenced by groundwater.

The behaviour of having many aggregations should be beneficial to the trout in case of a catastrophe wiping out fish in one portion of the stream. It would be more advantageous for fish to aggregate in several locations thus decreasing the likelihood of mortality caused by localized disturbances. It may also be advantageous for some fish to have a more isolated overwintering strategy.

Movement Details

I found fish in a large proportion (84-87 %) of the locations showed no movement. The spatial stability of trout in the fall and winter is similar to the findings of Heggenes *et al.* (1991a). When fish did move, most movements were over 100 m. This general pattern represents trout staying in one area for long periods of time until making longer moves.

The number of movements trout made decreased from summer to winter. The significant seasonal decrease in movement parallels the decrease in temperature and a shift from summer to staging and overwintering habitat. This shift in behaviour is also reflected by the decrease in mean number of moves that individuals made as the year progressed. Heggenes *et al.* (1991a), however, found no significant ($P<0.05$) decrease in movements during winter. This, however, appeared to be because they found movements very limited throughout the entire year (Heggenes *et al.* 1991a).

The differences that I found in the number of movements made between years in October and November may be due to differences in temperatures between the two years. The larger number of moves in October of 1992 than October 1991 may have been due to the warmer water temperatures in that year.

Macrohabitat Use

In most seasons and sites, pools dominated macrohabitat use. The only time pools were not the dominant habitat type used was in the North Ram River during the summer-early fall period. This predominant use of pools is similar to the findings of other researchers (Hartman 1965; Cunjak and Power 1986). Some researchers, however, have found trout used pools less in the winter (Logan 1963).

As temperatures decreased, macrohabitat use changed. As I expected, the trout in the North Ram River almost doubled their use of pools, while decreasing their use of shallower runs and riffles. The use of pools in 1992, which was later in the year than the tracking of 1991, showed another increase in the use of pools over the early fall-winter period of 1991. Thus, the use of pools increased from summer to winter while the use of shallower runs and riffles decreased.

This signifies a shift from a feeding to a sheltering behaviour. A similar shift was also observed by Hartman (1965), Tschaplinski and Hartman (1983), and Cunjak and Power (1986). This change to higher pool use is also related to the findings of Chisholm *et al.* (1987) that brook trout selected areas that had a maximum water velocity of 15 cm/s or less. These low water velocities were primarily found in pools. Hartman (1965) also found young steelhead shifted to higher use of pools in winter. Meyers *et al.* (1992) also found trout overwintering in low velocity water, and Baltz *et al.* (1991) found trout using significantly lower water velocities in November than in the summer. Similar findings were made by Cunjak and Power (1986). This conforms to the theory of energetic cost minimalization for position choice (Smith and Li 1983, Bachman 1984, Fausch 1984) where in the summer, the trout would want to be close to the fastest water to feed on drifting invertebrates, but during winter, since trout need to feed little, it would not be economical for them to expend the energy necessary to stay in the faster water of riffles and runs. By living in pools, trout may avoid the dangers of frazil and anchor ice which occur more in the turbulent water of riffles and runs (Ettema 1982), but may still be susceptible to the dangers posed by hanging dams.

In Onion Creek, although use of pools increased slightly and use of runs decreased seasonally, the pattern was not as prevalent as in the North Ram River. This is because many of the trout used the same habitat in the winter, as they did in the summer, since much of the creek is influenced by springs or snow bridging. The habitat of Onion Creek is stable throughout the year and the undercut banks and overhanging brush provide excellent cover for trout. Onion Creek also has a lower gradient than the North Ram River, providing better overwintering habitat. This is supported by Chisholm *et al.* (1987) who found 13 of 15 (87 %) radiotagged brook trout overwintered in low gradient (<1.5 %) reaches of streams.

Macrohabitat Preferences

The macrohabitat preferences of trout reflect the habitat use of these fish, with pools being preferred in all sites and seasons and runs and riffles being avoided in most sites and seasons (riffles were preferred in North Ram River during summer-early fall 1991). Similar to habitat use, preferences changed seasonally. The increase in preferences for pools and decreased in preferences for shallower habitats during fall and winter further illustrates the seasonal changes in habitat needs.

If the preference values truly illustrate the preferences of the fish, then the preference values for various sites should not differ significantly even if the habitat available is much different. The trout should choose the same habitat, pools for instance, whether they are widely available or scarce. If the preferences differ between sites, it is likely that the data does not reflect a fish's absolute preference but rather the best habitat available in that area. Preferences did differ significantly ($P<0.05$) between the North Ram River and Onion Creek during the summer-early fall season, but not during the late fall-winter season. Thus, during the summer-early fall period, the fish were likely not all in the habitat they preferred. Population densities may differ between the two systems so that in the one with the higher density of fish, or possibly in both drainages, many individuals get forced into suboptimal habitat. This would be the result of the aggressive territorial behaviour which trout exhibit during this season. The dominant fish would hold the most preferred feeding positions while less dominant fish would use less preferred sites. As water temperatures decrease, however, and the metabolism slows, the fish feed less and the aggressive behaviour subsides. Territorial behaviour breaks down and the trout then aggregate in preferred habitat. This pattern is suggested because during the late fall-winter season the preferences for macrohabitat between drainages did not differ significantly indicating that fish were choosing the same habitat despite the differences in availability.

Then the question remains, do the macrohabitat preferences of trout change seasonally, or is optimal overwintering habitat the same as optimal feeding habitat, but optimal feeding habitat is only held by the dominant cutthroat trout during the summer and early fall. Since competition is unlikely during winter, it is probable that the preferences I found during that season are true preferences. It is not possible for us to determine whether the preferences I calculated from summer habitat use are true preferences unless competition was removed as a variable and a wide range of habitat was available. Further research is necessary to provide these answers.

Examining preferences of macrohabitat (pools, runs, and riffles), however, may be a poor indicator of true preference, since pools, for instance, can be broken down into other parameters such as depth, velocity and substrate which cooccur with pools. By examining preferences of each of these parameters, water velocity, depth, and substrate, one may be better able to identify which single, or combination of parameters the fish really prefer.

Seasonal Microhabitat Use and Preference

Depth Use

I found that trout shifted to deeper habitats during the winter in the North Ram River, but not in Onion Creek. A selection for relatively deep water during the winter was also found by Chisholm *et al.* (1987), and Baltz *et al.* (1991) observed that juvenile trout used deeper water in November than in Summer.

The decrease in depth of water used in Onion Creek during the winter is similar to that found by Heggenes *et al.* (1991b) and Logan (1963). Heggenes *et al.* (1991b) found trout used deeper pools less, and inhabited significantly lower water depths (mean 18 cm) in the winter. Meyers *et al.* (1992) also found trout using relatively shallow (mean 73 cm) water depths when deeper areas were available in other stream stretches.

Depth Preferences

In all seasons trout preferred relatively deep water. Preference for water over 80 cm and a negative preference for water depths under 40 cm was a general trend. Hartman (1965) also noted that salmonids preferred the deepest water available.

During 1991, preferences for water depth did not significantly ($P<0.05$) change between sites or seasons. Thus although availability of water depths varied, the fish still choose the same water depths. This also illustrates that although water depth use decreased in Onion Creek while the opposite was true in the North Ram River, the preferences and the patterns of preferences were not different. I suggest that during fall and winter, the trout may prefer water depths over a certain threshold. That threshold likely occurs somewhere between 40 cm and 80 cm. It is likely that as long as the fish is in a water depth that is above the threshold that they will be satisfied with that habitat and not move to find a better location. I suggest this because fish showed strong preferences for water depths over 40-80 cm in all seasons and sites (Figures 3-18 and 3-19). The depth preference did not gradually increase as water depths increased as would be expected if fish preferred the deepest habitat, but leveled off above the 1-40 cm category in 1991 and the 41-80 cm category in 1992.

Cover Use

Our hypothesis that use of cover would increase during winter was rejected. In the North Ram River, I found that cover was used significantly ($P<0.05$) less after Sept. 15 than before that date. This is contradictory to the findings of Hartman (1965), Cunjak and Power (1986) and Logan (1963) who found cover used more in winter than summer. Our findings, however, are similar to those found in a British Columbia stream, where cutthroat trout used significantly lower amounts of cover in the winter than summer (Heggenes 1991b). This stream, however, likely did not receive surface ice cover because of its mild climate. Surface ice could be an important cover type during winter which would increase the availability of cover in colder climates, such as the Ram system.

Use of cover by cutthroat trout in Onion Creek was very high in the summer and continued to be high in the winter. Thus I did not observe an increase in cover use during the winter because use of cover was already very high in the summer (trout were found near cover in almost every observation, in both seasons).

Excluding ice cover, almost all of the overwintering areas used by fish in 1992 (in the North Ram River) did not have cover present. This is similar to the findings of Meyers *et al.* (1992) of surface ice providing the only cover during winter. I believe the presence of frazil and anchor ice is the reason why trout use less cover where warm water is not present. This is supported by the heavy use of cover during staging, before the onset of ice formation, and the significant ($P<0.05$) decrease thereafter. The only places where cover was used (other than surface ice) in the North Ram drainage was in areas where warm water was present, but by the end of December, there were no trout in areas with cover, other than surface ice. This, however, is likely just a coincidence in that none of the areas with groundwater had cover, rather than a negative selection for cover, since anchor ice could not affect the cover in the areas with groundwater.

While the decrease in cover use in the North Ram River was probably linked to frazil and anchor ice formation, the lack of a decrease in cover use in Onion Creek was also probably due to differences in habitat type and a lack of frazil and anchor ice in some sections. Much of Onion Creek was kept above 0.0°C during the winter by springs or had surface ice cover. These factors prevented frazil and anchor ice formation in many areas, thus, in much of Onion Creek fish couldn't be forced out of cover by ice exclusion as they were in the North Ram River.

In the North Ram drainage, large organic debris (branches and logs) was the main type of cover used in the fall, while in Onion Creek undercut banks were most commonly used. This difference in cover use is due to the cover availability present in the two drainages.

Substrate Use

Substrate use changed seasonally in both drainages. In the North Ram River, use of smoother substrates increased and use of rougher substrates decreased from the summer-early fall period to the late fall-winter period. These seasonal substrate changes were probably due to a less equal use of water velocity and macrohabitat types, in particular, the significant ($P<0.05$) increase in pool use as temperatures decreased. This is supported by Baltz *et al.* (1991) who found surface and mean water column velocities positively correlated with substrate size. This would indicate that slower water in pools would be correlated with the presence of fine substrate such as silt and riffles would contain larger substrate sizes which were used less in winter. I consider it unlikely that the cutthroat trout were choosing winter habitat based on substrate, but that substrate is a covariate of water velocity which trout used to choose winter habitat. Sand and silt were also selected in brook trout overwintering areas (Chisholm *et al.* 1987) and dominated brown trout overwintering areas (Meyers *et al.* 1992). Baltz *et al.* (1991). also found indications that smaller substrates were selected by rainbow trout during November than summer.

Substrate Preference

The seasonal trend of increased use of smoother substrates and decreased use of rougher substrates was also a general pattern in substrate preferences. As mentioned above, this appears to be due to the increased use of pools and lower water velocities during the winter season where finer substrates seem to occur more.

Although the preferences for many of the rougher substrate categories decreases during the late fall-winter season of 1991, they were still positively preferred in 1991, while they were not in 1992. I think that this is because many of the fish were not in their final overwintering areas when tracking was completed at the end of October, 1991.

Overall Preferences

The preference values for individual fish are shown to illustrate how different individual preferences can be. Some authors (White and Garrott 1990) suggest that if individual fish show significantly different preferences they should not be grouped. I report both individual and grouped preferences for several reasons. Individual preferences can show the variability or lack of variability of preferences for habitat. If there is very little variability in individual preferences (as in water depth category 1-40 cm Figure 3-19) in a category then it is likely that individuals are making a choice to use or not to use that particular category. If the variability is large, it is likely that the individuals just use the category randomly (as in water depth category 40-80 cm Figure 3-19), and are really showing no preference. Thomas and Taylor (1990) suggest that resources for which there is little variability in individual preferences may be more critical to manage than those with more variability. In some ways the preference for the grouped data is more meaningful than that for the individuals. For instance, since the fish moved little during winter they usually were found in few categories of water depth. So for those categories, they show a strong positive preference. For the other categories which were not used, however, the individual has a strong negative preference. The fish may prefer water depths over a certain threshold and be satisfied with its position as long as it is at a depth above that threshold. Thus, the individual avoidance of deeper water categories are misleading. In these cases the preferences shown for grouped data may be more representative of the population than just the individuals. Valuable information can be obtained from both the individual and the grouped preferences.

If individuals move little, then the preferences for the grouped data may be more representative of the population than the individual preferences. This is because, in many instances, fish may use habitat which is of lower value than its preferred habitat. Although better habitat may be available, it may not be worth the dangers of predation or energetic expense for the individual to keep searching until it finds the best habitat. It will just settle for adequate habitat. This does not mean that better habitat is negatively preferred just because it is not used by all individuals. In this case, as with our threshold theory, it is then best to look at the habitat use of a large number of individuals as I have done in this study and to make inferences from the grouped data as well as the individuals.

Depth appears to be a more dominant factor in the choice of habitat than does macrohabitat (pool, riffle, run). Macrohabitat, however, appears to be a more dominant factor in choice of position than substrate type. Water velocity and water temperature appear to be two factors which may also be very important in a fish's choice of position. Water velocity is also likely as important if not more important than water depth, at least as long as water depths are over a certain minimum threshold. The importance of water temperature in winter position choice may be variable. If frazil ice occurs in the stream, it is likely a very important factor, if it does not, then water temperature is probably not as important a factor in habitat choice. Water temperature and frazil ice production also appear to be of great importance in determining whether or not cover will be used. If frazil ice occurs then cover in the form of logs and branches may not be used unless warm water is available in some sections of stream. The factors involved in position choice appear to vary with circumstances, but the trout are also very flexible and can adapt to optimize use of the resources available to them.

Conclusion

This research broadens our understanding of trout overwintering in several aspects. Our observation that cutthroat trout begin aggregating in September might require early closures of angling seasons or other measures to protect them at this vulnerable time. The information I have gathered on two stage movements to overwintering areas indicates that the habitat needs of trout are broader than most have anticipated, and that trout are very flexible, changing their behaviour to suit the habitat available to them. The data I have gathered on the effects of frazil and anchor ice should act as a platform to encourage increased research into this neglected aspect of trout biology.

The major conclusion of this study is that trout do make shifts in habitat use at the end of summer, but they don't always simply make one shift. The initial habitat shift is linked to metabolic changes in response to decreasing temperatures, while the second is strictly due to environmental changes. The first shift in habitat use, which is associated with decreased feeding, aggressiveness, and territoriality, is not a new finding, but the second shift is new, and has not been considered in fisheries management. The presence of frazil and anchor ice in montane streams and rivers forced fish to make the second habitat shift, and use different habitat than in areas with milder climates. The number of montane streams affected by frazil and anchor ice is probably very large, and in these areas exist some of North America's most valuable trout streams. Ice and groundwater influx are major factors determining habitat suitability and carrying capacity in these streams and they are factors that should be considered when planning habitat improvement projects and modeling habitat suitability.

To optimize winter habitat improvement, I suggest that not only the parameters of water depth, velocity, and substrate be examined, but water temperature and behavioural aspects of overwintering should be examined to a greater extent. Aggregation appears to play a major role during the overwintering period, yet it is little understood. Do trout aggregate in winter only because preferred habitat is scarce, is it a response to predation, or is there another underlying reason for this behaviour? Is this behaviour dominant enough for fish to leave preferred habitat for less preferred areas where aggregation occurs? If overwintering habitat is to be constructed for fish, it is important to understand how this behaviour is involved in the choice of habitat.

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Chapter Four

General Conclusions

General Conclusions

The data gathered in this study represent the best documentation of spawning and overwintering movements of non-anadromous trout to date. They provide a better understanding of the factors that cause movements and the variability in those movements. Cutthroat trout make major movements three times during the year. The move from overwintering to spawning areas, from spawning to summer feeding areas, and from feeding areas to overwintering areas. In places where conditions are severe, like the North Ram River, the movement from summer feeding habitat to overwintering areas involves two stages, but in areas where conditions are less severe, like upper Onion Creek, only one movement takes place.

Just as I found variability in patterns of movement to overwintering areas, there was variability in patterns of movement to spawning areas. The finding that radiotagged cutthroat trout moved both up and downstream to spawning areas in both migratory and resident life history types should renew interests in the processes involved in choice of spawning habitat and homing to spawning areas. It is unlikely that genetic differences caused any of the variation in movement patterns observed because there has not been sufficient time for genetic differences to arise. Since these trout were stocked 20 - 40 years ago, it is evident from these patterns that trout are very flexible and can quickly adapt to changes in habitat. Although the spawning movement patterns are contradictory to those observed by many researchers (Cope 1956, Bjornn and Mallet 1964,Allan 1978,Shepard *et al.* 1984) this is likely because spawning movements have not been thoroughly examined, using methods like radiotelemetry, rather than that the behaviour of trout in the Ram system is unique.

It is likely that the patterns of pre-spawning movements are related to the availability of overwintering habitat, more than any other factor. If overwintering habitat is limited in portions of river systems, the fish would be forced to migrate in whatever direction or distance necessary to find spawning habitat. Thus, if overwintering habitat is improved, spawning mortality may be decreased, and populations may grow at a faster rate.

The detailed pattern of movement I observed during spawning has not been reported previously. In the Ram River, trout appeared to spawn within a small lenght of stream perhaps similar to a spawning territory, of approximately 400 m. The females made redds, and the males attended several redds within this size of area, perhaps attempting to spawn with all females in their territory. The area that is used for spawning likely depends on the quality of habitat, with fish using a smaller area where habitat is excellent, and using a larger area where habitat is poorer. The upper limit of spawning area size would probably be limited by the physiological demands of moving long distances. Thus, if better habitat is available, trout likely spawn in a smaller area and expend less energy, leaving spawning areas while in better body condition, leading to a lower probability of mortality and a greater likihood of repeat spawning in following years. Thus enhancement of spawning habitat should lead to more productive populations.

As I suggest that the distance fish moved to spawning areas is related to habitat availability, I also suspect that distances moved after spawning rely heavily on availability of habitat. I have found that in resident spawners, long movements to spawning areas are not necessarily reflected in long movements from spawning to summer habitat, but that fish may spend their summer in the same area where they spawned. This is similar to the ideas of Miller (1954, 1957) that given suitable habitat, fish will live in one stretch of stream their entire lives. It is likely, however, that the stability of fish would vary with competition and variance of individual behaviours.

The cutthroat trout exhibited a spawning pattern that has not previously been described. The fish changed from a sedentary life style during late winter, to one characterized by sudden movement to spawning areas in May. Once at spawning areas, the fish made many small movements in a limited reach of stream. After spawning, the fish again made sudden movements to their summer habitat, where they made little if any subsequent movements.

The occurance of resident and migratory spawning strategies in the same section of river has aslo not been documented previously. Because both life history types can occur in the same area, the spawning patterns of tributary spawners may not reflect all or a majority of spawning trout.

I found that movements and habitat use during fall and winter are interrelated. Distances and directions moved to staging and overwintering habitats vary with habitat availability. The timing of movements varied with changes in environmental factors (water temperature, ice conditions). The real reasons for movements of fish to overwintering areas may be based on physiological changes, but the physiological changes are caused by environmental stimulii.

One of our major findings is that trout did not always make one simple habitat shift in the fall. I found that decreasing water temperatures were associated with trout moving out of summer habitat and into staging pools by the last half of September. The staging pools that trout shifted to have similar attributes as overwintering habitat described by other researchers (Cunjak and Power 1986, Chisholm *et al.* 1987, Meyers *et al.* 1992). I suggest that at some temperature threshold trout shifted from a strategy of feeding and growth, to a strategy of conserving energy and finding protection from the perils of winter, this was also suggested by Cunjak and Power (1986). Due to the harsh winter conditions in the Ram system, however, I found a second stage of overwintering movement behaviour. This second movement stage was caused by anchor ice excluding staging pools. Thus, the severity of climate appears to be a factor in the distance moved to overwintering areas.

The cutthroat trout did not move long distances to staging or overwintering areas as other researchers found (Bjornn and Mallet 1964) who studied trout movements in areas with harsh climates. It is likely that the length of movements were related to the quality of overwintering habitat. Thus, trout are very adaptable to their environment, moving whatever distance or direction necessary to fulfill their needs.

One of the factors which had an affect on winter habitat use was frazil ice production. Factors that made overwintering habitat distinct was that they didn't have frazil or anchor ice present. Due to the common presence of frazil and anchor ice in the Ram drainage, groundwater played a very important role in winter habitat selection.

During fall and winter, trout used and preferred pools and deep water (deeper than 40-80 cm). It is not possible, however, for us to determine whether the preferences I calculated for trout before they aggregated (or in the summer-early fall period) are true preferences unless competition was removed as a variable and a wide range of habitat was available. Since trout probably don't compete for food or habitat during near freezing temperatures, the preferences in late fall and winter should be fairly accurate.

Although substrate use changed seasonally with a trend of smoother substrates being used and preferred more in winter while rougher substrates were used and preferred less, it is unlikely that substrate was a major factor involved in choice of overwintering habitat. I suggest that, since researchers (Baltz *et al.* 1991) have found surface and mean water column velocities positively correlated with substrate size, that fish are choosing winter habitat on the basis of water velocity more than substrate size. Trout have been found to use lower velocity water in the fall and winter than during summer (Cunjak and Power 1986, Baltz *et al.* 1991). The fish would expend less energy in near still waters than in higher velocity areas, and have less likelihood of being affected by frazil and anchor ice which occurs more in turbulent, high velocity waters (Ettema *et al.* 1982).

From our findings I suggest that the major factors involved in choice of position during the winter are water depth, velocity, temperature, and cover. The importance of water temperature in winter position choice is probably variable with the likelihood of frazil and anchor ice occurrence. In low gradient, low elevation streams it may not be as important as in areas where gradient is higher and anchor ice occurs more. Water temperature and frazil ice production may determine whether cover is used or not. If frazil ice occurs, logs and branches may not be used for cover unless warm water is available in some sections of stream.

In conclusion, it appears that movements are mostly made out of necessity to find adequate habitat, whether for spawning, feeding, or overwintering. The distance and direction that fish will move to find needed habitat is highly variable. Improvement of habitat would probably decrease the movements fish make as Hunt (1974) found. Improved habitat should correlate to less energy expended on movements, energy which can be channeled into growth and reproduction. Thus, improving habitat would help populations to grow to their carrying capacity, fulfilling a major goal of fisheries managers.

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